

*Passerella
iliaca*FRENCH:
Bruant fauve
SPANISH:
Chingolo zorruno

Fox Sparrow

When John James Audubon found a Fox Sparrow for the first time on its breeding grounds in southern Labrador in 1834, he had no idea that he was looking at one of North America's most geographically variable birds. With 18 subspecies divided into 3 or 4 distinct groups, this species shows extensive variation that has been the focus of 3 intensive monographs on external morphology, skeletal characteristics, and genetics (Swarth 1920, Linsdale 1928a, Zink 1986). Its life-history characteristics also vary greatly across its range.

The Fox Sparrow is a common but shy inhabitant of streamside thickets and chaparral across the northern boreal and western montane regions of North America. Habitat preference varies geographically, with each of the major groups preferring nesting locations with different plant communities. Fox Sparrow populations also vary in migratory distance and route; individuals nesting in the Sierra Nevada of California migrate only short distances, mostly altitudinally, while those from Alaska migrate long distances, with some traveling over open ocean. Populations also vary in their song types; while northern and eastern Fox Sparrow populations sing 1 or 2 song types each, western populations sing 3 or 4; commonly heard calls (contact notes) also vary geographically, differences largely correlating with the major groups.

**The
Birds of
North
America**
Life Histories for
the 21st Century



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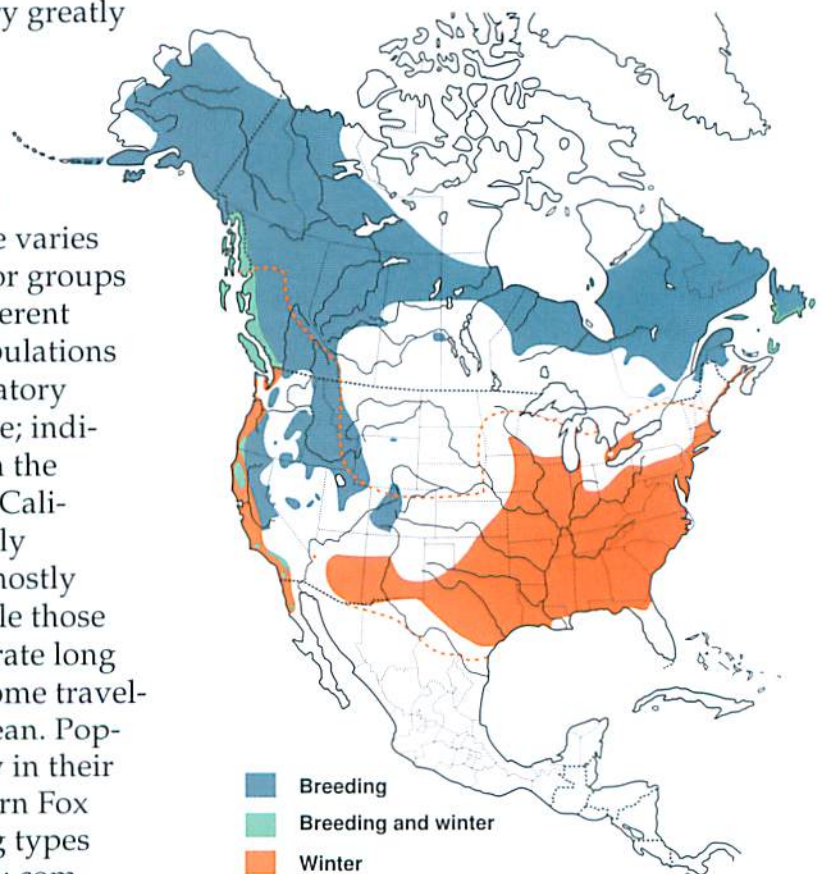


Figure 1.
Distribution of the Fox Sparrow. This species winters very locally north and south to the dashed line. See text for details.

This sparrow's large geographic distribution, relative abundance, and extreme geographic variation in plumage, morphology, habitat preference, migratory behavior, and vocalizations make it ideal for comparative evolutionary studies. While several modern studies have focused on Fox Sparrow systematics, song, and migration, many aspects of the life history of this species remain unknown. Its shy habits and preference for dense vegetation have made the collection of life-history data difficult.

DISTINGUISHING CHARACTERISTICS

Large sparrow (emberizid), 15.0–18.5 cm long (Rising 1996), 25–49 g mass, sexually monomorphic. In general, breast and flanks have rufous to sooty-brown streaks, some of which form a central spot on the breast. Wings, upper tail-coverts, and rectrices rufous to dark sooty brown. Mantle coloration gray with rufous streaks, or unstreaked gray to sooty brown. Bill bicolored, with upper mandible blackish brown and basal edges dull orange or yellow. Lower mandible orangish or yellowish with grayish-brown tip. Bill size variable but conical and moderate to heavy in size. Largest-billed Fox Sparrows have deeper bills than all other North American sparrows. Feet and legs pinkish brown to reddish brown; iris dark brown to reddish brown. Through careful consideration of geographic variation in plumage (see Systematics: geographic variation, below), most individuals can be identified to 1 of the 4 major groups of subspecies: (1) Red Fox Sparrow (*iliaca* group), reddish-plumaged birds, with streaked backs and comparatively shorter tails; (2) Sooty Fox Sparrow (*unalaschensis* group), dark-brown or sooty-plumaged birds with comparatively shorter tails and medium-sized bills; (3) Slate-colored Fox Sparrow (*schistacea* group), longer-tailed birds with gray backs, reddish wings and tails and medium-sized bills; and (4) Large-billed Fox Sparrow (*megarhyncha* group), longer-tailed birds with gray backs, reddish wings and tails, and large bills.

SIMILAR SPECIES

Distinguished from Song Sparrow (*Melospiza melodia*) by (generally) larger size (wing 73–92 mm, tail 62–91 mm), shorter deeper bicolored bill, lack of streaking on upperparts (western subspecies), indistinct or no dark streak on malar region, and ventral streaking composed of broader, more triangular markings (Rising 1996, Pyle 1997).

DISTRIBUTION

THE AMERICAS

Breeding range. Figures 1 and 2. Red Fox Sparrow (*iliaca* group) breeds from n. and w. Alaska (north to Brooks Range), n. Yukon, sw. Northwest Territories, extreme sw. Nunavut, n. Manitoba, n. Ontario, n. Quebec, n. Labrador, and n. Newfoundland south to southern interior of Alaska, central interior and n.-central British Columbia (south to Dease Lake and Peace River parklands), s.-central Alberta, n. (locally south to central) Saskatchewan, n.-central Manitoba, n.-central Ontario, s. Quebec (south to Abitibi, Laurentides, and Chaudière-Appalaches regions, Anticosti I., and Magdalen Is.), extreme nw. Maine, nw. New Brunswick, Prince Edward I., coastal Nova Scotia, and s. Newfoundland (Godfrey 1986; Adamus 1987; Rising 1987, 1996; Erskine 1992; Semenchuk 1992; Bisson and Limoges 1996; Smith 1996; Am. Ornithol. Union 1998).

Sooty Fox Sparrow (*unalaschensis* group) breeds on e. Aleutian islands (west to Unalaska), Shumagin and Semidi Is., Alaska Peninsula, Kodiak and Middleton Is., Kenai Peninsula, s.-coastal and se. Alaska, and coastal districts of British Columbia (including Queen Charlotte Is.) south to Destruction and Lopez Is. of extreme nw. Washington (Rising 1996, Am. Ornithol. Union 1998).

Slate-colored Fox Sparrow (*schistacea* group) breeds from central interior British Columbia (Crowsnest Pass), sw. Alberta (Waterton Lakes Park), south through central and e. Washington, n.-central and e. Oregon, Idaho, and w. Montana to n. and central Nevada (extending west to White Mtns. of extreme e.-central California), central Utah, w. and (locally in) central Wyoming, and throughout western half of Colorado (Oakleaf et al. 1992, Rising 1996, Smith et al. 1997, Am. Ornithol. Union 1998, Potter and Roth 1998, Adamus et al. 2001, Nevada Breeding Bird Atlas [BBA] 1997–2000 unpubl.).

Large-billed Fox Sparrow (*megarhyncha* group) breeds from central portions of w. Oregon and from s.-central Oregon south through California, including northern and inner Coast Ranges, Siskiyou and Warner Mtns., and in Sierra Nevada to Mono Lake district and Greenhorn Mtns., and mountains of s. California (Big Pine Mtn., Mt. Pinos, San Gabriel, San Bernardino, San Jacinto, and Palomar Mtns. and Cuyamaca Peak) and extreme w. Nevada (Small 1994, Rising 1996, Am. Ornithol. Union 1998, Adamus et al. 2001). Recently found by Erickson and Wurster (1998) breeding in Sierra San Pedro Mártir, Baja California.

Winter range. Figure 1. Red Fox Sparrow (*iliaca* group) winters principally east of the Great Plains from se. Minnesota, s. Wisconsin, s. Michigan, southernmost Ontario, central Pennsylvania, se. New

York, n. Massachusetts, s. New Hampshire, coastal Maine, coastal New Brunswick (very rare), coastal Nova Scotia (local), and coastal s. Newfoundland (local) south to eastern half of Texas, s. Louisiana, s. Mississippi, s. Alabama, and n. Florida. Small numbers also winter in the Pacific Coastal Region (rare), principally in interior from Washington south to nw. Baja California. Winters irregularly farther north and west of main range in e. North America and rarely to s. Florida. Casual or very local in interior California, s. Arizona, s. New Mexico, and Sonora, Mexico (Russell and Lamm 1978, Rising 1996, Am. Ornithol. Union 1998, Garrett et al. 2000, Christmas Bird Count [CBC] data), but occasionally observed elsewhere in central and w. North America, including Wainwright and the Barrow region of Alaska and on Banks I., Nunavut (Garrett et al. 2000), north of its breeding distribution.

Sooty Fox Sparrow (*unalaschensis* group) winters in Pacific coastal region from se. Alaska (rarely) and central British Columbia south through Washington and Oregon to s. California, rarely to nw. Baja California. Has occurred casually to se. Arizona (Chiricahua Mtns.; Phillips et al. 1964) and there is 1 record from winter of 1994–1995 from Burlington, ND (Garrett et al. 2000). Also recorded during winter on Nunivak, the Pribilofs, St. Lawrence I., and Point Barrow in n. Alaska (Rising 1996, Garrett et al. 2000).

Slate-colored Fox Sparrow (*schistacea* group) winters from n. interior California, central Arizona, and n. New Mexico south to s. California, n. Baja California, and rarely in s. Arizona, n. Sonora, and w. Texas (Rising 1996, Am. Ornithol. Union 1998, Garrett et al. 2000). Also occurred during winter or spring migration in w. Nebraska (Am. Ornithol. Union 1957), Manitoba (Am. Ornithol. Union 1957), and New York (Buckley 1974).

Large-billed Fox Sparrow (*megarhyncha* group) winters from central California south to s. California and n. Baja California (Am. Ornithol. Union 1998, Garrett et al. 2000), and there are 2 records from w. Arizona (Phillips et al. 1964).

OUTSIDE THE AMERICAS

Red Fox Sparrows (*iliaca* group) recorded at least twice in w. Greenland (Boertmann 1994) and 5 times in Europe, including Borg, Iceland, on 5 Nov 1944 (Cramp and Perrins 1994); Copeland I. (Down), Ireland, on 3–4 Jun 1961 (Wilde 1962, Dymond et al. 1989); Mellum I., Germany, on 13 May 1949 (Niethammer et al. 1964, Cramp and Perrins 1994); Scharhorn I., Germany, on 24 Apr 1977 (Schmid 1979); and Liguria, Italy, in 1936 (Brichetti and Massa 1984, Cramp and Perrins 1994). Schmid (1979) suggested that the Red Fox Sparrow found on Scharhorn I. was likely a ship-assisted vagrant

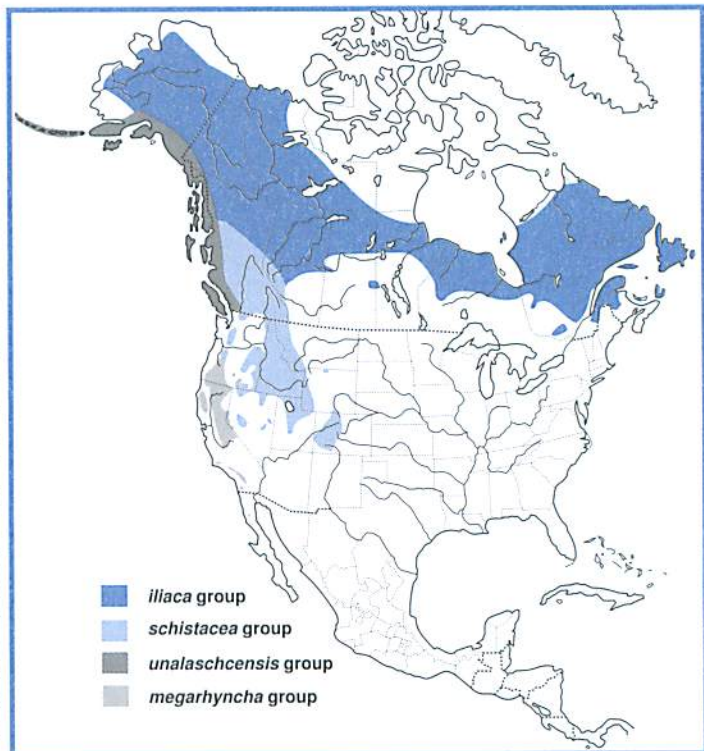


Figure 2. Breeding distribution of the Fox Sparrow's 4 subspecies groups.

and that E. Stresemann thought that the Mellum I. record was also ship-assisted. Sooty Fox Sparrow (*unalaschensis* group) recorded in Russia (Uel'kal', Kresta Bay, Chukchi Peninsula, on 28 Jun 1961; Rising 1996, Garrett et al. 2000) and in Japan (once in fall and once in winter; Brazil 1991, Am. Ornithol. Union 1998).

HISTORICAL CHANGES

On west slope of Oregon Cascades, logging sometime after 1941 created large expanses of brushy new growth (Banks 1970). On 21 Jun 1960, Banks (1970) collected a *P. i. fulva* in Linn Co., OR, where breeding Fox Sparrows were previously unknown. On 24 Jul 1968, at another locality in Linn Co., OR, Harry Nehls and William Thackberry found a breeding population of *P. i. megarhyncha* and collected 1 individual (Banks 1970). Banks (1970) attributed these new breeding records to logging operations opening up new habitat suitable for Fox Sparrows and questioned whether this habitat alteration brought *P. i. megarhyncha* and *P. i. fulva* into sympatry in this region.

FOSSIL HISTORY

Two records from e. North America, including one from a late Pleistocene (approx. 11,300 yr before present) cave deposit, Sinkhole No. 4 at New Paris,

Bedford Co., PA (Guilday et al. 1964) and another from the Natural Chimneys, north of Mt. Solon, VA (Wetmore et al. 1962). The Wetmore (1962) specimen is the symphysis of the lower mandible of a Fox Sparrow, similar to that of the *iliaca* subspecies. In w. North America, at least 4 fragmentary Fox Sparrow fossils have been found. Two Fox Sparrow lower mandibles found in Pleistocene deposits at Rancho La Brea, CA, were reported by Dawson (1948). The ramus of one of these specimens measures 25.2 mm, corresponding to subspecies *stephensi*, *brevicauda*, or *megarhyncha*, whereas the other measures 22 mm, corresponding to measurements of subspecies *iliaca*, *townsendi*, *fuliginosa*, *canescens*, and some populations of *megarhyncha* (Dawson 1948). Also, a fragmentary Fox Sparrow lower mandible was found in fossiliferous asphalt accumulations near Carpinteria, Santa Barbara Co., CA by Miller (1932). Although Miller (1932) was unable to determine to which subspecies this fragment belongs, he acknowledged that the fossil did not represent any of the forms with an extremely large bill (*stephensi*, *mariposae* [= *megarhyncha*], *brevicauda*) or slightly enlarged bill (*iliaca*). Instead, mandible is from one of the subspecies with an intermediate bill size (*townsendi*, *fuliginosa*, *fulva*). A tarsometatarsus found at the same site was also referable to *P. iliaca* (Miller 1932).

SYSTEMATICS

GEOGRAPHIC VARIATION

Varies geographically in plumage coloration, relative lengths of wing and tail, and bill shape and size. Subspecies generally fit into 1 of 4 groups (see Distinguishing characteristics, above), which are well defined by plumage (Swarth 1920), morphometrics (Linsdale 1928a, Zink 1986), and genetics (Zink 1994, Zink and Weckstein in press). Within each of these 4 species groups, geographic variation in plumage and morphology is considerable. *Iliaca* group characterized by bright-reddish coloration with a grayish crown and nape, tail shorter than wings, and a medium-sized bill (Swarth 1920); this group also shows a pale triangular patch above end of pale submoustachial-stripe, which is not obvious in other Fox Sparrow groups (Rising 1995). Within *iliaca* group, subspecies vary from east to west, with western birds tending to have a grayer head and nape and browner ventral streaking and malar-stripe (Rising 1995, 1996). *Unalaschcensis* group consists of dark-brown to sooty-plumaged birds with tail shorter than wings and a medium-sized bill (Swarth 1920); face of those in this group nearly uniform brown in both lores and submoustachial area, lacking typically light-colored lores

found on birds in the other 3 groups (Rising 1995, Zink and Kessen 1999). Subspecies in *unalaschcensis* group vary clinally in both size and coloration. Coloration varies from dark brown with a reddish wash in the north to sooty brown in the south (Swarth 1920). Within *unalaschcensis* group, subspecies in the north are generally larger bodied and larger billed than those in the south (Rising 1996). *Schistacea* group consists of birds with reddish wings and tail, brownish gray to slaty-gray crown and back, tail usually longer than wings and medium-sized bill (Swarth 1920, Rising 1996). *Schistacea* group varies clinally from north to south, with amount of gray in crown and back and bill size increasing from north to south (Swarth 1920). *Megarhyncha* group consists of birds with reddish wings and tail, grayish-brown to ashen-gray crown and back, tail usually longer than wings, and large-sized bill (Swarth 1920, Zink and Kessen 1999). Large bill size and call note (see Sounds: vocalizations, below) distinguishes birds in *megarhyncha* group from others. *Megarhyncha* group has an almost identical pattern of variation to that of *schistacea* group, with amount of gray in crown and back and bill size increasing from north to south (Swarth 1920, Zink and Kessen 1999).

Zink's (1986) analysis of allozymes found little or no protein differentiation among morphologically and geographically diverse samples of western populations of Fox Sparrows, whereas analyses of mitochondrial DNA (mtDNA) detected significant amounts of genetic structure, identifying 4 groups of Fox Sparrows corresponding to those defined by plumage and morphology (Zink 1994, Zink and Blackwell 1996). Although phylogenetic relationships among the 4 groups of Fox Sparrows are equivocal (Zink and Weckstein in press), *megarhyncha* and *schistacea* groups, which are most similar in plumage and morphology, are almost certainly not each other's closest relatives (Zink 1994, Zink and Blackwell 1996, Zink and Weckstein in press). Patterns of mtDNA variation suggest that hybridization between these 4 groups is limited between all pairs of taxa except *megarhyncha* and *schistacea* groups (Zink 1994). Zink (1994) found evidence of a narrow contact zone between these 2 groups along the interface of the Great Basin and Sierra Nevada-Cascade axis. *Megarhyncha* and *schistacea* groups also intergrade morphometrically, although over a broader area than the contact zone (Zink 1994). A complex pattern of hybridization exists at the interface of *unalaschcensis*, *iliaca*, and *schistacea* groups, where they meet in British Columbia, Yukon, Alberta, and Alaska (Williamson and Peyton 1962, Webster 1975, Zink 1994). Nine of 139 individuals from this region carried the "wrong" mitochondrial DNA haplotype, most

likely indicating low levels of hybridization (Zink 1994). More genetic work needed, especially at interfaces between Fox Sparrow groups.

SUBSPECIES

Subspecific taxonomy has changed over time from 16 subspecies recognized by Swarth (1920) and Linsdale (1928a) to 18 subspecies recognized by Am. Ornithol. Union (1957). Many of these are weakly differentiated taxa. Swarth (1920), studied external morphology and recognized 3 main groups of subspecies: *iliaca* group (*iliaca*, *altivagans*), *unalaschcensis* group (*unalaschcensis*, *insularis*, *sinuosa*, *annectens*, *townsendi*, *fuliginosa*), and *schistacea* group (*schistacea*, *megarhyncha*, *mariposae*, *stephensi*, *brevicauda*, *fulva*, *canescens*, *monoensis*). A few subspecies were not yet described at the time of his study. Subsequently, Am. Ornithol. Union (1957) recognized 18 subspecies of Fox Sparrow including: *P. i. iliaca*, *P. i. zaboria*, *P. i. altivagans*, *P. i. unalaschcensis*, *P. i. insularis*, *P. i. sinuosa*, *P. i. annectens*, *P. i. townsendi*, *P. i. fuliginosa*, *P. i. olivacea*, *P. i. schistacea*, *P. i. swarthi*, *P. i. canescens*, *P. i. fulva*, *P. i. monoensis*, *P. i. megarhyncha*, *P. i. brevicauda*, and *P. i. stephensi*. Two additional subspecies, *P. i. mariposae* (Swarth 1918) and *P. i. chilcatensis* (Webster 1983) have been described but are not widely recognized.

Based on morphometric and allozyme data, Zink (1986) hypothesized that *iliaca*, *unalaschcensis*, and *schistacea* groups were at least 3 distinct species; however, his analysis of mtDNA variation (Zink 1994) suggested that the Fox Sparrow is in fact 4 species, Red Fox Sparrow, *P. iliaca* (including races *P. i. zaboria* and *P. i. iliaca*), Sooty Fox Sparrow, *P. unalaschcensis* (including *P. u. unalaschcensis*, *P. u. insularis*, *P. u. sinuosa*, *P. u. annectens*, *P. u. townsendi*, and *P. u. fuliginosa*), Slate-colored Fox Sparrow, *P. schistacea* (including *P. s. altivagans*, *P. s. olivacea*, *P. s. schistacea*, *P. s. swarthi*, and *P. s. canescens*), and Large-billed Fox Sparrow, *P. megarhyncha* (including *P. m. fulva*, *P. m. brevicauda*, *P. m. mariposae* [= *megarhyncha*], *P. m. monoensis*, and *P. m. stephensi*). Analysis of MtDNA only resolves these 4 major groups and was unable to distinguish subspecies as defined by morphology (Zink 1994). Rising (1996) recognized 3 groups, lumping *schistacea* and *megarhyncha* groups. Am. Ornithol. Union (1998) recognized the 4 groups at informal rank of subspecies group and suggested that, based on genetic evidence (Zink 1986, 1991, 1994) and morphology (including plumage coloration), the 4 groups each may represent a biological species. Before these groups are recognized as separate species, additional study is needed in contact zones between groups, especially along hybrid zone between *schistacea* and *megarhyncha* (Am. Ornithol. Union 1998).

Red Fox Sparrow (*iliaca* group)

P. i. iliaca Merrem, 1786. Breeds from ne. Manitoba, n. Ontario, n. Quebec, n. Labrador, and n. Newfoundland south to n.-central Ontario, s. Quebec, extreme nw. Maine, nw. New Brunswick, Prince Edward I., coastal Nova Scotia, and s. Newfoundland (Swarth 1920, Am. Ornithol. Union 1957, Adamus 1987, Rising 1987, Erskine 1992, Bisson and Limoges 1996). Winters from s. Wisconsin, s. Michigan, southernmost Ontario, central Pennsylvania, se. New York, n. Massachusetts, s. New Hampshire, coastal Maine, coastal New Brunswick (very rare), coastal Nova Scotia (local) and coastal s. Newfoundland (local) south to s. Mississippi, s. Alabama, and n. Florida (Am. Ornithol. Union 1957, CBC data). *P. i. iliaca* can be distinguished from all subspecies in *schistacea* group by different proportions in wing and tail lengths (wing longer than tail in *iliaca*, wing equal to or shorter than tail in *schistacea* group) and overall bright-ruddy plumage coloration. The much brighter hue of reddish markings, sharply contrasting red-and-gray dorsal streaking, and heavier and more stubby bill distinguish *iliaca* from all subspecies within *unalaschcensis* group. *P. i. iliaca* distinguished from *altivagans* by greater general size and brighter, more ruddy coloration, with more sharply defined dorsal streaking (Swarth 1920).

P. i. zaboria Oberholser, 1946. Breeds from n. Manitoba west through extreme sw. Nunavut, sw. Northwest Territories, n. Yukon, to nw. and interior Alaska and south to n.-central Manitoba, central Saskatchewan, s.-central Alberta, and n. British Columbia (south to Dease Lake, Peace River parklands; Oberholser 1946, Am. Ornithol. Union 1957, Godfrey 1986). Winters east of Great Plains from se. Minnesota, central and e. Iowa, se. Kansas, and central and e. Oklahoma south to s. Texas, Louisiana, Mississippi, Alabama, and n. Georgia. Rarely winters in w. U.S. (Am. Ornithol. Union 1957). This subspecies was split from *iliaca* by Oberholser (1946), because its upperparts, including wings and tail, average darker and more grayish or sooty. Oberholser (1946) also noted that *zaboria*'s reddish-brown breast-spots usually smaller, less numerous, and duller than those in *iliaca*. However, Rising (1995) states that although very gray individuals are probably *zaboria*; *iliaca* and *zaboria* cannot be reliably separated.

Sooty Fox Sparrow (*unalaschcensis* group)

P. i. unalaschcensis Gmelin, 1789. Breeds from Unalaska I. (in e. Aleutians) to Shumagin and Semidi Is. and Alaska Peninsula (Swarth 1920, Am. Ornithol. Union 1957). Winters from s. British Columbia south to extreme s. California and rarely to n. Baja California (Swarth 1920, Am. Ornithol. Union 1957,

Garrett et al. 2000). Two morphologically diagnosable groups of *unalaschensis* winter in California: one with long, pointed bill and pale-brownish plumage that is ashy in tone and one with plumage darker in appearance and plumbeous in tone, with a shorter/heavier bill (Swarth 1920). Birds from Alaska Peninsula show range of variation, possibly indicative of intergradation with *sinuosa* to the southeast and *insularis* to the south (Swarth 1920).

P. i. townsendi Audubon, 1838. Breeds on islands and mainland in se. Alaska from Glacier Bay south to Queen Charlotte Is., British Columbia (Swarth 1920, Am. Ornithol. Union 1957). Winters along coast from breeding range south to central California (Swarth 1920, Am. Ornithol. Union 1957). Coloration much darker and more rufescent, and breast-spots larger and more crowded than other subspecies from *unalaschensis* group to the north and brighter colored and less sooty than *fuliginosa* to the south (Swarth 1920).

P. i. fuliginosa Ridgway, 1899. Breeds on mainland coast of se. Alaska (south of Stikine River) and coastal British Columbia, except Queen Charlotte Is., south to nw. Washington (Ridgway 1899, Swarth 1920, Am. Ornithol. Union 1957). Winters from sw. British Columbia south to coastal central California (Ridgway 1899, Swarth 1920, Am. Ornithol. Union 1957). Darker and less rufescent when compared to similar *P. i. townsendi* to its north. Breast-spots dark sooty brown, and larger and more confluent than in other forms (Ridgway 1899).

P. i. annectens Ridgway, 1900. Breeds on coast of s. Alaska, from Cross Sound to north shore of Yukutat Bay (Ridgway 1900, Am. Ornithol. Union 1957). Most winter along coast of central California (Swarth 1920). Intermediate in plumage and morphology between *sinuosa* to the north and *townsendi* to the south. Plumage brighter and more ruddy than *sinuosa* but not as dark as *townsendi* (Swarth 1920). Breast-spotting sparser than *townsendi* (Swarth 1920). Slightly smaller in bill and body size than subspecies to the north and larger than *townsendi* to the south (Swarth 1920).

P. i. insularis Ridgway, 1900. Breeds on Kodiak I. and winters southward along Pacific Coast to extreme s. California (Ridgway 1900, Am. Ornithol. Union 1957). Similar to *unalaschensis*, but brighter, ruddier, and more uniform above (Swarth 1920). Spots on chest larger and deeper brown. Under tail-coverts tinged with buff (Ridgway 1900). Bill of *insularis* is heavier in structure than *sinuosa* but about the same bulk as *unalaschensis* (Swarth 1920).

P. i. sinuosa Grinnell, 1910. Breeds in Prince William Sound and Kenai Peninsula districts and on Middleton I. (Grinnell 1910, Am. Ornithol. Union 1957). Winters south along Pacific slope of s. Cali-

fornia (Swarth 1920). Bill of *sinuosa* more slender, and breast-spotting larger and heavier than in *unalaschensis*. Plumage more reddish than *unalaschensis*, but less than in brighter-colored *insularis* and darker-colored *annectens* and *townsendi* (Grinnell 1910, Swarth 1920).

P. i. chilcatensis Webster, 1983. Described from mainland of se. Alaska and adjacent Canada. According to Webster (1983), *chilcatensis* breeds from Chilkat River area of British Columbia and Alaska southeast to Tewart area of British Columbia and winters from coastal Oregon south through coastal counties of n. California to San Francisco Bay region, although Grinnell and Miller (1944) cited additional specimens from Monterey, Los Angeles, Siskiyou, Shasta, and Lassen Cos. A few wintering specimens examined by Webster (1983) were collected farther north, one on Prince of Wales I., AK, and one at Puget Sound, WA (Webster 1983). Webster (1983) split *chilcatensis* from *fuliginosa*. Although Swarth (1920) did not formally recognize the division of *fuliginosa* into 2 subspecies, he suggested that *fuliginosa* might need subdivision and called birds like those described by Webster (1983) "non-typical *fuliginosa*." According to Webster (1983), *chilcatensis* is less reddish, duller in color and has a shorter tail than *fuliginosa*. However, most authors (Zink 1994, Rising 1996, Zink and Kessen 1999), do not recognize *chilcatensis*, presumably because *chilcatensis* is an arbitrary point on a cline and not a distinct taxon.

Slate-colored Fox Sparrow (*schistacea* group)

P. i. schistacea Baird, 1858. Breeds from se. British Columbia (Crownsnest Pass) and sw. Alberta (Waterton Lakes Park) south through high mountains of the Great Basin region, including n.-central and e. Oregon (Cascade Mtns. south to Warm Springs; Howard; Wallowa Mtns.), and w. Montana (Judith River, Red Lodge) south to n.-central and ne. Nevada (breeding recently confirmed in mountains of ne. Humboldt Co. and central Elko Co.; Nevada BBA 1997–2000 unpubl.) and sw. Wyoming (Fort Bridger), and western half of Colorado (Cochetopa Creek; Swarth 1920, Am. Ornithol. Union 1957). Winters along coast, coastal ranges, and both central and s. Sierra Nevada of s. California (Swarth 1920, Garrett et al. 2000). *P. i. schistacea* has slate-colored head, slate-colored back washed with brown (mouse gray), brown wings and rump, rusty-brown tail, and breast and flanks heavily spotted with dark brown (Rising 1996). Bill of *schistacea* smaller than that of birds in *megarhyncha* group and overlaps considerably with other subspecies in *schistacea* group.

P. i. altivagans Riley, 1911. Breeds from interior central British Columbia southeast to mountains of se. British Columbia and sw. Alberta (Am. Ornithol.

Union 1957). Winters principally in Cascades and Sierra Nevada of California, coastal s. California, and nw. Baja California (Am. Ornithol. Union 1957). Plumage coloration similar to *schistacea*; however, middle of back brown rather than mouse gray, and wings and tail more reddish brown (burnt umber; Riley 1911). Although Riley (1911) noted similarity between *altivagans* and *schistacea*, Swarth (1920) considered *altivagans* to be a member of *iliaca* group. However, both Rising (1986) and Zink (1994) classify *altivagans* as a member of *schistacea* group, as indicated by both voice (Martin 1977) and mitochondrial DNA (Zink 1994). Populations within *altivagans* have considerable variation, with some darker-colored birds, dark reddish brown above and heavily spotted below, and other lighter-colored birds, predominantly grayish above and sparsely spotted below (Swarth 1920). These variants may indicate intergradation with neighboring subspecies (Swarth 1920). Darker birds are probably intergrades with *unalaschcensis* (*fuliginosa*), lighter ones are intergrades with *iliaca* group (with *P. i. zaboria*). *P. i. altivagans* also known to intergrade with *schistacea* near Banff, Alberta (Am. Ornithol. Union 1957), and *olivacea*, as noted by Swarth (1920), who found some duller birds that had less reddish coloration and tail length roughly equal to wing length.

P. i. canescens Swarth, 1918. Breeds in central Nevada (Shoshone, Toiyabe, Monitor Mtns.) and extreme central e. California (White Mtns.; Swarth 1918, Am. Ornithol. Union 1957). Breeding recently confirmed over somewhat broader range in central Nevada, including mountains of se. Churchill, n. Nye, and s. and e. White Pine Cos. (Nevada BBA 1997–2000 unpubl.). Winters in s. California, n. Baja California, and s. Arizona (Swarth 1920, Am. Ornithol. Union 1957). Similar to *schistacea* but grayer (Swarth 1918).

P. i. olivacea Aldrich, 1943. Breeds from sw. and s.-central British Columbia (Mt. McLean, Nelson) south through central and e. Washington on east slopes of Cascade Mtns. of Washington, eastward to at least Blue Mtns. of Washington and Oregon, mountains of ne. Washington, and probably to n. Idaho and nw. Montana (Aldrich 1943, Am. Ornithol. Union 1957). Winters in interior California (Tehama Co., Piute Mtns.) and n. Baja California (Sierra Juárez). *P. i. olivacea* similar to *schistacea* in Wyoming, but darker and more olivaceous (Aldrich 1943). *P. i. olivacea* is dark hair brown to olive-brown above, rather than light hair brown to light olive-brown, and edges of wing- and tail-feathers and upper tail-coverts are Brussels brown to Argus brown, rather than cinnamon brown (Aldrich 1943). *Olivacea* also similar to *fulva* of central Oregon but more brownish with dark hair-brown to olive-brown plumage above, rather than cinnamon brown

to Prout's brown. Bill of *olivacea* shorter and more slender than *fulva*'s (Aldrich 1943). Intergrades with *schistacea* to its east (Aldrich 1943).

P. i. swarthi Behle and Selander, 1951. Breeds from se. Idaho (Bannock and Bear Lake Cos.) through n.-central Utah (Raft River Mtns., Deep Creek Mtns., Wasatch Mtns. south to Sanpete Co.; Behle and Selander 1951, Am. Ornithol. Union 1957). Winter range unknown (Behle and Selander 1951, Am. Ornithol. Union 1957). Grayer on head and back, and breast-streaking heavier and less rufescent than *schistacea*. Most similar to *canescens*, but grayer (Behle and Selander 1951). Behle and Selander (1951) suggest that in northern, northwestern, and eastern portions of its range, *swarthi* is connected by clines to *schistacea*. Probably also connected by clines to *canescens* (Behle and Selander 1951).

Large-billed Fox Sparrow (*megarhyncha* group)

P. i. megarhyncha Baird, 1858. Breeds from sw. Oregon (Onion Mtn., Robinson's Butte) south through central n. California (Siskiyou Mtns. at Del Norte Co. line and Mt. Orr, head of Dog Creek) and Sierra Nevada of California south to Kearsarge Pass (Swarth 1920, Am. Ornithol. Union 1957). In central Sierra Nevada (Mono Lake district) breeds only on western flank (Swarth 1920, Am. Ornithol. Union 1957). Winters in central and s. California and nw. Baja California (Am. Ornithol. Union 1957). Intermediate in bill size, tail length, and general body size between *monoensis* and *stephensi*. Characteristics and geographic distribution of *megarhyncha* as recognized by Zink (1986) and Rising (1996) are identical to those of *mariposae*, as recognized by Swarth (1918). Zink (1986) and Rising (1996) have accordingly synonymized Swarth's (1918) *mariposae* with *megarhyncha*, the older name. Connected to *stephensi* by a cline of morphological and plumage variation (Zink 1986).

P. i. stephensi Anthony, 1895. Breeds in s. Sierra Nevada from Sierras of s. California; Hume and Horse Corral Meadow (Fresno Co. through Tulare Co.), summit of Mt. Pinos (Ventura Co.), San Gabriel Mtns. (Los Angeles Co.), San Bernardino Mtns. (San Bernardino Co.) and San Jacinto Mtns. (Riverside Co.; Swarth 1920) to n. Baja California in Sierra San Mártir (Erickson and Wurster 1998). Primarily winters at lower elevations in s. California (Am. Ornithol. Union 1957). *P. i. stephensi* most similar to *megarhyncha*, but generally larger in body size and has a larger bill (Anthony 1895). Relatively enormous bill of *stephensi* distinguishes it from all other Fox Sparrows. *Stephensi* can be told from *brevicauda* by its more slenderly pointed bill, more grayish plumage coloration, and longer tail. *Stephensi* is southernmost extreme in cline of increasing bill

size, increasing tail length, and more grayish plumage coloration, when compared with other subspecies in *megarhyncha* group (Swarth 1920, Zink 1986).

P. i. monoensis Grinnell and Storer, 1917. Breeds in California's Mono district on eastern flank of central Sierra Nevada (Woodfords, Mammoth, Benton) and in Mineral Co., NV (Walker River Range; Am. Ornithol. Union 1957). Winters in central interior and s.-coastal California, south to nw. Baja California (Am. Ornithol. Union 1957). Closely resembles *megarhyncha*, but has a less robust bill and slightly (paler) ashier gray on upper parts (Grinnell and Storer 1917). Bill thicker and dorsal coloration paler than in *schistacea* (Grinnell and Storer 1917).

P. i. brevicauda Mailliard, 1918. Breeds in northern and inner coast ranges of California, from Yolla Bolly Mtns. (at junction of Trinity, Tehama, and Mendocino Cos.) south to Snow Mtn. (Colusa Co.) and Mt. Sanhedrin (Mendocino Co.; Mailliard 1918, Swarth 1920, Am. Ornithol. Union 1957). Winters in coastal central and s. California (Swarth 1920, Am. Ornithol. Union 1957). *Brevicauda* is relatively large billed and is similar to *stephensi*; however, head, neck, back, and breast-spots more fuscous brown, rather than the mouse gray of *stephensi* (Mailliard 1918). Body size nearly identical to *stephensi*, but with a relatively shorter tail, hence the name *brevicauda* (Mailliard 1918).

P. i. fulva Swarth, 1918. Originally described from a specimen collected in Warner Mtns. of Modoc Co., CA. *Fulva* breeds from central Oregon, east of Cascades (Sisters, Keno, Steens Mtns.) into extreme ne. California (Modoc, Lassen Cos.; Swarth 1920, Am. Ornithol. Union 1957). Winters from sw. California to n. Baja California (Am. Ornithol. Union 1957). Bill of *fulva* intermediate in size between *schistacea* and *megarhyncha*, which is similar but more slender and attenuated than that of *monoensis* (Swarth 1918, 1920). Wing and tail measurements similar to *schistacea*, but shorter than in *megarhyncha* (Swarth 1918, 1920). Overall plumage coloration of *fulva* more brownish than *megarhyncha* and *monoensis*, which is similar to *schistacea* (Swarth 1918, 1920).

P. i. mariposae Swarth, 1918. Originally described from a bird collected near Chinquapin, in Yosemite National Park, CA. According to Swarth (1918, 1920), *mariposae* breeds from Siskiyou Co., CA, from the head of Little Shasta River, south at least to Yosemite National Park region on west slope of Sierra Nevada and to Kearsarge Pass on east slope of Sierra Nevada. *Mariposae* is intermediate in bill structure between *monoensis* and *stephensi* and is nearly identical in plumage coloration to *canescens*, *monoensis*, and *stephensi*. Zink (1986) and Rising

(1996) synonymized *mariposae* with *megarhyncha*, the name that has priority for this form.

RELATED SPECIES

Historically, Fox Sparrow thought to be closely related to Song Sparrow (Paynter 1964), because of their similarity in plumage coloration, morphology, song, and nesting habits (Swarth 1920, Rising 1996, Patten and Fugate 1998). Linsdale (1928b) considered Song Sparrow to be so similar to Fox Sparrow that he merged genus *Melospiza* into genus *Passerella*. Zink (1982) suggested that this generic merger would obscure significant amount of genetic differentiation found in comparisons of proteins (allozymes) between these taxa. Furthermore, mtDNA sequence analyses (Zink and Blackwell 1996) suggested that *Passerella* was not at all closely related to *Melospiza*. Zink and Blackwell's (1996) mtDNA sequence data suggested that *Passerella* was most closely related to a clade of sparrows including *Zonotrichia* and *Junco*. Most recent molecular evidence (also mtDNA sequences) identified American Tree Sparrow (*Spizella arborea*) as sister to Fox Sparrow, with this pair sister to a *Junco-Zonotrichia* clade (J. Klicka pers. comm.). While phylogenetic data strongly supported that *Spizella arborea*, *Junco*, and *Zonotrichia* were closest living relatives of *Passerella*, genetic distance between *Passerella* and its closest living relatives was relatively high (greater than 11% mtDNA sequence divergence; Zink and Weckstein in press), indicating that no close extant relatives exist (J. Klicka pers. comm.).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

All populations migrate; some long distances, others short-distance altitudinal movements. Subspecies with largest wing and pectoral girdle bones (e.g., 3 northwesternmost nesting subspecies) migrate the longest distances (Swarth 1920, Zink 1987, Bell 1997; see Fig. 3), southwesternmost subspecies the shortest distances. Mean migration distance of *P. i. iliaca*, an eastern intermediate-distance migrant, is 1,123 km (Brewer et al. 2000).

TIMING AND ROUTES OF MIGRATION

Iliaca group. Late migrant in fall and early migrant in spring, reaching s. Great Lakes area by first week of Mar, ending migration by late Apr (Speirs 1985, Temple and Cary 1987, Garrett et al. 2000). Mean spring arrival date in Newfoundland (9 Apr; Threlfall and Blacquiere 1982) placed *P. i. iliaca* among earliest spring migrants there. Late dates in s. Ontario include 3, 4, 12, and 25 May (Speirs 1985). Spring departure dates for n.-central

Texas range from 25 Mar to 5 May (Pulich 1988). Usually departs Louisiana by late Mar (Lowery 1974).

Band-recovery data indicate that breeders from Canada's Maritime Provinces move southwest to winter on U.S. mid-Atlantic Coast (Brewer et al. 2000). Early records of migrants in s. Ontario include 22 and 28 Sep (Speirs 1985). Fox Sparrows breeding west of Hudson Bay probably winter in se. U.S. (Brewer et al. 2000). Extreme arrival dates in Texas range from 15 Oct to 3 Nov (Pulich 1988); in Louisiana, 19 Oct (Jackson 1992) and 1 Nov (Oberholser 1938).

Mean movement for banded and recaptured Red Fox Sparrows varied from 107 km for individuals banded in their hatching year (HY) to 1,009 km for those banded after hatching year (AHY; Brewer et al. 2000). Maximum movement for a HY Red Fox Sparrow was 2,126 km, for an AHY bird 2,204 km (Brewer et al. 2000).

***Unalaschcensis* group.** Spring movements not well known, but bulk of movements most likely occur in late Mar and early Apr (Garrett et al. 2000), with birds arriving on breeding grounds by late Apr and early May (Gabrielson and Lincoln 1959). During fall, birds in *unalaschcensis* group arrive in California as early as mid-Sep (Garrett et al. 2000) with peak movement in early Oct (Desante and Ainley 1980, Garrett et al. 2000).

Migratory route apparently differs among subspecies of *unalaschcensis* group. *P. i. annectens* and *P. i. townsendii* migrate along coast; *P. i. unalaschcensis*, *P. i. insularis*, and *P. i. sinuosa* most likely make a transoceanic flight via a great circle route (shortest route between 2 points on surface of a sphere; Swarth 1920, Bell 1997; Fig. 3). If Fox Sparrows migrate via great circle routes, then migratory route of the population migrating from Unalaska I. (*P. i. unalaschcensis*) to s. California is among the longest ocean crossings undertaken by a land bird (Bell 1997). *P. i. fuliginosa*, as well as other *unalaschcensis* group subspecies, undoubtedly undergo altitudinal migration (Swarth 1920).

Three easternmost subspecies within *unalaschcensis* group (*P. i. annectens*, *P. i. townsendii*, and *P. i. fuliginosa*) exhibit a pattern of leapfrog migration, in which southernmost breeding subspecies (*P. i. fuliginosa*) migrates the shortest distance and the northernmost (*P. i. annectens*) migrates farthest to the south, leapfrogging over winter ranges of more southerly nesting subspecies (Swarth 1920, Zink 1987, Bell 1997; Fig. 3). Three westernmost subspecies (*P. i. unalaschcensis*, *P. i. insularis*, *P. i. sinuosa*), which winter the farthest south and migrate the longest distances, nest at approximately at same latitude as *P. i. annectens* and therefore do not fit pattern of leapfrog migration outlined by Swarth (1920, Bell 1997).

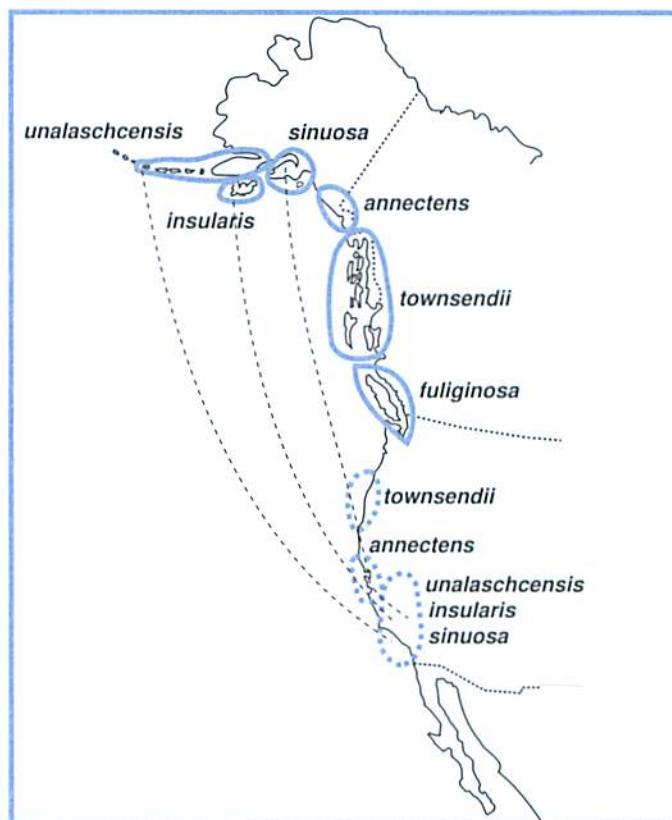


Figure 3. Distribution of the subspecies in the *unalaschcensis* group of Fox Sparrows on breeding and wintering grounds. Dotted lines show approximate transoceanic migratory routes of the northernmost subspecies. From Swarth 1920 and Bell 1997.

***Schistacea* group.** Little known (Garrett et al. 2000). However, Slate-colored Fox Sparrows migrate much earlier than Red Fox Sparrows, with fall migrants showing up as early as late Aug (Hoover Dam, NV/AZ, 29 Aug) and spring migrants arriving on breeding grounds as early as late Mar (Garrett et al. 2000). Migrant specimens of *P. i. olivacea* have been identified from Stanley, WY, 23 Aug; Kemmerer, WY, 16 May; Ruby Mtns., NV, 18 Aug; Hart Mtn., OR, 14 Sep; and Beswich, CA, 19 Sep (Aldrich 1943).

Members of this group vary from nearly sedentary, with altitudinal movements, to fully migratory (Cramp and Perrins 1994). During fall, birds in the *schistacea* group migrate downslope from higher altitudes (Swarth 1920), and then migrate to the southwest, wintering mostly in California and n. Baja California (Garrett et al. 2000).

***Megarhyncha* group.** Of all Fox Sparrows, those in *megarhyncha* group migrate the earliest, beginning in late Aug, with bulk of movement in Sep (Garrett et al. 2000). However, some also remain on territory as late as mid-Sep (Garrett et al. 2000). Thick-billed

Fox Sparrows also migrate early in spring, with small numbers appearing at oases in California deserts as early as mid-Feb but mainly in late Mar through late Apr (Garrett et al. 2000). Nearly all Thick-billed Fox Sparrows winter in s. California and nw. Baja California (Garrett et al. 2000).

MIGRATORY BEHAVIOR

From Terrill 1968. Migrates at night and usually arrives on breeding grounds during early-morning darkness. Regularly migrates over large expanses of open water. Migratory "fallouts" associated with severe snowstorms (Terrill 1968). In Newfoundland, males and females apparently migrate and arrive on breeding grounds at same time (Blacquiere 1979).

CONTROL AND PHYSIOLOGY

From Weise 1962. Individuals kept in photoperiod chambers set at 9 h of light and 15 h of darkness for 18 mo exhibited a migratory response during spring and fall, including fat deposition and onset of *Zugenruhe*. Fat deposition and *Zugenruhe* declined and eventually disappeared by following autumn and winter, while migratory conditions developed anew in second spring of this experiment. Weise (1962) attributed fall declines and spring renewals of migratory conditions in Fox Sparrows to changes in temperature, because photoperiod was kept constant.

HABITAT

BREEDING RANGE

***Iliaca* group.** Prefers thick cover, especially brushy woodland edges, grown-up fields, cut-over woodland, and scrubby woods. In ne. Canada, prefers almost impenetrable stands of low shrubby black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), tamarack (*Larix laricina*), aspen (*Populus* spp.), birch (*Betula* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.) bordering wet boggy areas (Terrill 1968, Rising 1987). In Alaska and nw. Canada, alder and willow thickets in spruce forest, often among white spruce (*Picea glauca*; Austin 1968). In Newfoundland, highest densities in tuckamoor (clumps of wind-blown stunted conifers) and scrub forest; also common in successional old fields, cut-over and burned areas; less common in continuous coniferous forest, and both rocky alpine and coastal barrens (Blacquiere 1979). In Newfoundland, also nests in closed-climax balsam fir, black spruce, and white spruce forest, with some bare ground for foraging a prerequisite (Threlfall and Blacquiere 1982).

***Unalascensis* group.** Found from beach to timberline in mostly deciduous thickets, preferring

willow and blackberry (*Rubus* spp.) thickets, lush riparian vegetation, and streamside brush (Linsdale 1928a, Williamson and Peyton 1962, Austin 1968, Louisiana State University Museum of Natural Science [LSUMNS]).

***Schistacea* group.** In the Great Basin, prefers to nest in impenetrable riparian thickets (usually near watercourses or mountain meadows) consisting of alder, water birch (*Betula occidentalis*), willows, currants and gooseberries (*Ribes* spp.), and rose (*Rosa* sp.; Salt 1957, Austin 1968, Zink 1986). *P. i. altivagans* breeds in both small dense clumps of stunted spruce and patches of tangles of alder and false hellebore (*Veratrum* spp.) growing above treeline (Austin 1968).

***Megarhyncha* group.** Nests in montane chaparral consisting of brushy fields, occurring from 1,220 m to 3,000 m (Zink 1986). Likes burned-over forest land at a stage of recovery with heavy growth of brush (Austin 1968). At sites in Sierra Nevada, postfire, Fox Sparrow densities change as brushy fields of chaparral mature (Bock and Lynch 1970, Bock et al. 1978). Approximately 10 yr after a fire, montane chaparral reached a density sufficient to support the species (Bock and Lynch 1970). Most common plants in this montane chaparral include green-leaf manzanita (*Arctostaphylos patula*), mountain whitethorn (*Ceanothus cordulatus*), and bush chinquapin (*Castanopsis sempervirens*; Austin 1968, Zink 1986, Burns and Hackett 1993). In Green Mtns., south of main Sierra Nevada, Fox Sparrow found in elderberry (*Sambucus* sp.) thickets (Zink 1986). At one site in Hume, Fresno Co., CA, nesting habitat consists of roughly 35% mixed coniferous forest and 65% chaparral (Burns 1988, Burns and Hackett 1993). Relative plant abundance in the chaparral at Hume was approximately 60% mountain whitethorn, 20% green-leaf manzanita, 10% sierra gooseberry (*Ribes roezlii*), and 5% bush chinquapin (Burns 1988, Burns and Hackett 1993). Proportions of different tree species in this same area included 45% giant sequoia (*Sequoiadendron giganteum*), 40% white fir (*Abies concolor*), 10% ponderosa pine (*Pinus ponderosa*), and 5% sugar pine (*Pinus lambertiana*; Burns 1988).

SPRING AND FALL MIGRATION

During migration, *Iliaca* group Fox Sparrow often scratches in leaf litter in open hardwood forest, where little or no ground cover (Austin 1968). Also likes swampy tangles and weedy stream borders (Austin 1968). In Colorado, found in lowland riparian shrublands (Andrews and Righter 1992). During migration (mainly during fall), *unalascensis* group regular in California's eastern deserts (Garrett et al. 2000). For *schistacea* group, during spring migration, mostly from late Mar through

late Apr, appears in small numbers in California's desert oases (Garrett et al. 2000). During migration through Colorado, found in wooded riparian areas (Andrews and Righter 1992). Among *megarhyncha* group, during early spring, Thick-billed Fox Sparrow appears at oases in California deserts (Garrett et al. 2000).

WINTER RANGE

***Iliaca* group.** Prefers thick cover of thickets and underbrush, especially brushy tangles on edge of woods and dense willow or weedy areas along streams (Terrill 1968).

***Unalascensis* group.** Prefers chaparral, ranging from arid to damp, spending much of its time in ground litter beneath screening cover of thick vegetation (Austin 1968). In s. California, predominates along with *schistacea*-group birds in relatively tall chaparral vegetation on cooler, more mesic north-facing slopes (Garrett et al. 2000). Common plant cover includes: thimbleberry (*Rubus parviflorus*), poison-oak (*Toxicodendron diversiloba*), nine-bark (*Physocarpus* sp.), *Ceanothus* spp., coyote bush (*Baccharis pilularis*), and salal (*Gaultheria shallon*); Grinnell and Miller 1944, Austin 1968).

***Schistacea* group.** In s. California, predominates along with *unalascensis*-group birds in relatively tall chaparral vegetation on cooler, more mesic north-facing slopes (Garrett et al. 2000).

***Megarhyncha* group.** Core wintering range consists of chaparral, with birds of this group predominating on warmer south-facing slopes dominated by chamise (*Adenostoma fasciculatum*) in s. California (Garrett et al. 2000).

FOOD HABITS

FEEDING

Main foods taken. In breeding season, adults: principally arthropods, including primarily insects, but occasionally spiders and also small mollusks (Linsdale 1928a). Also occasionally seeds, fruit, and plant matter (Linsdale 1928a, Grinnell et al. 1930, Austin 1932, LSUMNS, University of Washington Burke Museum [UWBM]). Outside the breeding season, adults more omnivorous—a mixture of fruits, seeds, insects, and occasionally buds of plants (Judd 1901, Linsdale 1928a, Grinnell et al. 1930, Schmid 1958, LSUMNS, UWBM). For nestlings: see Breeding: parental care, below.

Microhabitat for foraging. Nests and feeds in same microhabitat (see Breeding: nest site, below). Generally feeds in leaf litter; may pick insect food items off growing vegetation (Grinnell et al. 1930). In winter and during migration, feeds in leaf litter

under fairly thick cover (Austin 1968, Terrill 1968), either on borders of woods, second growth, or even among scattered brush cut from recently felled trees (Linsdale 1928a). During prolonged snowfall or freezing rain, may leave shelter of thickets and thick cover to forage in the open (Terrill 1968). During Mar at Patuxent Research Refuge in Maryland, 5–10 Fox Sparrows fed daily under a large willow oak (*Quercus phellos*), and many others were seen feeding under multiflora rose (*Rosa multiflora*) hedges (Schmid 1958).

Food capture and consumption. Forages in leaf litter and on bare ground using a “double-scratch” movement—both feet moved synchronously to disturb the ground and leaf litter (Hailman 1973, 1976). Apparently sees insects best when 15–30 cm away (Grinnell et al. 1930). May fly from perch to air to capture flying insects (Linsdale 1920, R. Zink pers. comm.).

DIET

Major food items. During breeding season: beetles and weevils (Coleoptera), fly larvae (Diptera), caterpillars (Lepidoptera), ants and bees (Hymenoptera), scale insects (Homoptera), spiders (Arachnida), millipedes (Diplopoda), small mollusks (Bivalvia and Gastropoda), and seeds and fruits of *Carex* sp., *Rubus* sp., *Potentilla* sp., *Diodia* sp., and serviceberry (*Amelanchier* sp.; Linsdale 1928a, Grinnell et al. 1930). Known to feed on dead and desiccating fish along beaches (Terrill 1968). On wintering grounds: fruits of American strawberry bush (*Euonymus americana*), red cedar (*Juniperus virginiana*), pokeweed (*Phytolacca americana*), blueberries (*Vaccinium* sp.), elderberries (*Sambucus* sp.), blackberries (*Rubus* sp.), grapes (*Vitis* sp.), witch hazel (*Hamamelis* sp.) buds, and seeds of ragweed (*Ambrosia* sp.), smart weed (*Polygonum* sp.), hounds tongue (*Cynoglossum* sp.), *Lythospermum* sp., *Panicum* sp., sorrel (*Rumex* sp.), *Phleum pratense*, and other “weeds” (Judd 1901, Linsdale 1928a, Terrill 1968). In spring and during migration, feed on arthropods and seeds (see Feeding, above) and withered, fallen fruits from previous year (Austin 1968). Individuals collected in Mar, Apr, and May had fruit seeds in their stomachs, including seeds of blueberries, elderberries, blackberries, grapes, and multiflora rose (Schmid 1958, Austin 1968). Stomachs commonly contain grit, gravel, or soil detritus (Linsdale 1928a, LSUMNS, UWBM, Bell Museum of Natural History [MMNH]).

Quantitative analysis. Recent data lacking. Analysis of stomachs from 10 individuals from Esmeralda Co., NV, however, indicates that Hymenoptera made up 71% of food items taken by Fox Sparrows during May, Coleoptera 16% (Linsdale 1928a). Stomachs of 2 *P. i. iliaca* collected in Apr

were almost completely filled with seeds plus parts of 2 ground beetles (Carabidae; Linsdale 1928a). Ground beetles and millipedes made up about 30% of food taken by migrant Fox Sparrows collected in the e. U.S. (Judd 1901, Terrill 1968). Stomachs of 127 Fox Sparrows collected Sep–Apr in e. U.S. contained 86% plant matter and 14% animal matter; seeds of berries and fruit skins made up 28% of food taken during winter; millipedes 20% of all food items taken during migration (Apr; Judd 1901). Of 36 specimens collected throughout the year, 80.5% of stomachs held seeds; 25% insect parts; 5.6% berries; 11.1% plant matter; and 8.3% grit, soil, or other detritus (LSUMNS, UWBM, MMNH).

FOOD SELECTION AND STORAGE

No information.

NUTRITION AND ENERGETICS

No information.

METABOLISM AND TEMPERATURE REGULATION

From Rogers and Rogers 1990. Evening and dawn body mass and fat class vary seasonally and in parallel ($p < 0.0001$, for all 4 comparisons). Fox Sparrow exhibits a seasonal increase in dawn body mass and visible fat class as midwinter approaches, and then a decrease in dawn body mass and visible fat class toward spring. Individuals overcompensate for nightly mass loss by storing more fat for an emergency energy supply as longer, colder nights of midwinter approach.

DRINKING, PELLET-CASTING, AND DEFECATION

No information.

SOUNDS

From the Gulf of St. Lawrence, Brewster (1883: 377) waxed enthusiastic about the song of the Red Fox Sparrow: "At all hours of the day, in every kind of weather late into the brief summer, its voice rises among the evergreen woods filling the air with quivering, delicious melody, which at length dies softly, mingling with the sighing of the wind in the spruces, or drowned by the muffled roar of the surf beating against neighboring cliffs. To my ear the prominent characteristic of its voice is richness. It expresses careless joy and exultant masculine vigor, rather than delicate shades of sentiment, and . . . is such a fervent, sensuous, and withal perfectly rounded carol that it affects the ear much as sweetmeats do the palate, and for the moment renders all other bird music dull and uninteresting by comparison."

Richness of whistled eastern song replaced by more burry quality in the West (see below).

Two primary sources of information are a master's thesis by Blacquiere (1979) and a series of papers by Martin (1977, 1979, 1980, 1990) based on his Ph.D. thesis (Martin 1976).

VOCALIZATIONS

Development. Two vocalizations heard from nestlings (Blacquiere 1979: 29). By young nestlings, in response to movement of or near nest, a 0.25- to 0.75-s high, thin *seep*, a continuous call modulated at 20–50 Hz between 6 and 10 kHz, like a continuous sine wave on a sonogram. By older nestlings, when handled, loud and harsh bursts of 6 or 7 notes in a second, evoking a vigorous response from adults, of *check* calls and "short rapid flights, and fluttering from branch to branch."

Songs learned, as revealed by local dialects (see below), and by mimicry. Western groups reported to mimic Olive-sided Flycatcher (*Contopus cooperi*) and Black-chinned Sparrow (*Spizella atrogularis*; Erickson and Wurster 1998), as well as a variety of other species (e.g., Hammond's Flycatcher [*Empidonax hammondi*] in Sierra Nevada; G. F. Budney unpubl.). No mimicry reported for Red forms in either literature or by L. Peyton (unpubl.) from extensive recordings in Alaska.

See also Phenology, below.

Vocal array. **MALE SONG.** Songs of eastern Red Fox Sparrow "like the soft tinkling of silver bells" (Judd 1901: 88), "not a note . . . [of] . . . which a human being cannot whistle" (Moore 1913: 182). Often reported to be ventriloquial (e.g., Townsend and Allen 1907). Best described from Newfoundland (Blacquiere 1979): Males typically have a single song type (of 169 individuals, 163 had a single song, 6 had 2 songs; see also Moore 1913). Number of whistled notes in song averages 11.7 ± 2.0 SD (range 7–22, $n = 175$ songs from 169 individuals), overall song duration $2.54 \text{ s} \pm 0.27$ SD (range 1.93–3.44, $n = 175$). Male always sings same sequence of whistled notes (or syllables) in his song, though last note sometimes left off, perhaps more so later in season; when especially agitated, male may omit a note in middle of song (Blacquiere 1979).

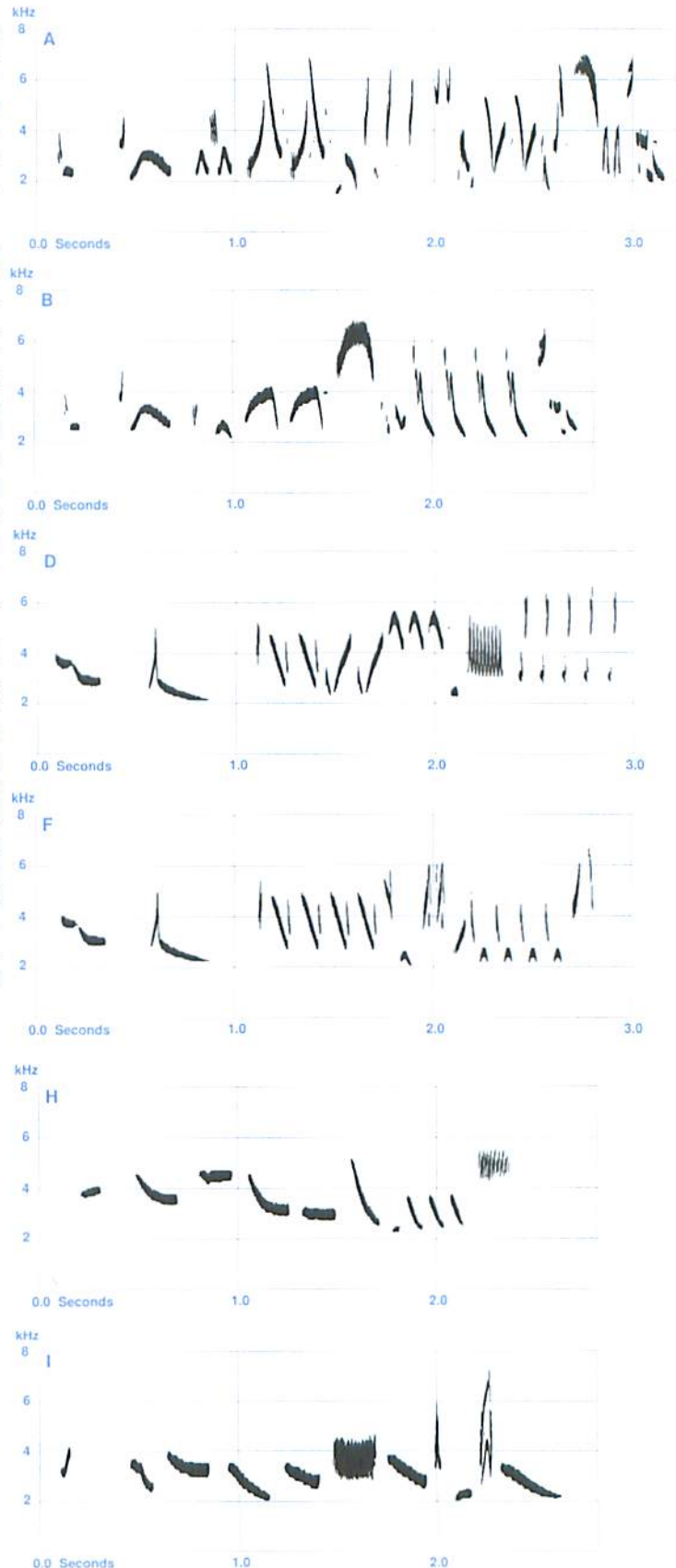
Newfoundland Red Fox Sparrows much like those in Nova Scotia (Naugler and Smith 1991). On Bon Portage I., each of 11 males had a single song type, and only 2 types occurred on island, 5 males with one type, 6 with the other. Same songs present in 1989 and 1990. Songs of Red forms in Alaska also largely whistled, and 3 selections in Peyton 1999, from Anchorage, Fairbanks, and Copper River drainage, all consist of a male singing a single song type (see Fig. 4), just as in Newfoundland and Nova Scotia.

In Alaska, most Red forms also sing only 1 song, but 2 songs are "not uncommon"; males would occasionally use one type during playback, 2 eventually sometimes after playback. One banded male retained same song for 3 consecutive years (L. Peyton unpubl.; males in Newfoundland and Nova Scotia studies were not banded, so similar information not available from those studies).

Songs vary geographically. In Newfoundland, songs on small islands only 2–4 km offshore are different from those on mainland. On mainland, songs seem to vary continuously over distance, with localities 200–300 km distant having highly distinct songs. Last half of song more consistent within locality and more distinctive between localities (Blacquiere 1979). In Alaska, Red forms also have song dialects; songs from Copper River drainage, for example, are different from those in rest of Alaska, and males from Copper River drainage do not respond to playback of songs from elsewhere, and vice versa. Where 2 dialects converge at Isabel Pass, males respond to both types (L. Peyton unpubl.).

Songs of Sooty, Slate-colored, and Thick-billed groups differ from those of Red group (see Fig. 4), though only Slate-colored has been studied in any detail (Martin 1976, 1977, 1979, 1980, 1990). Western birds also have characteristic rich tone and great amplitude (Martin 1977), but typically have more buzzy trills and fewer clear whistled notes, and they seem to mimic more, too (Garrett et al. 2000; Fig. 4). Males in Martin's n. Utah and s. Idaho study site had a repertoire of 3 or 4 song types (average 3.2 and 3.1 in 1973 and 1974, respectively; range 2–7). Number of syllables in a song ranged from 7 to 9. Males were also highly consistent in singing same repertoire of songs, even from year to year.

Figure 4. Songs of Fox Sparrows. A, B, D, F: Four of the 7 songs in the repertoire of a Thick-billed Fox Sparrow from Yuba Pass, CA, recorded 6 Jun 2001 by DEK. Full sequence of songs: A C A B A C A B D E F G D E F G D E F G D E B A C A B A B A B C A B A C F G D E F G D E F G D E B A C A B A B A B C A D E F E D F G D F G D E D, showing that songs with similar beginnings (A, B, C and D, E, F) tended to occur together. Terminal notes of B and F are strikingly similar to the familiar *klee-yer* call of Northern Flicker (*Colaptes auratus*), and the *piik* call of the American Robin (*Turdus migratorius*), respectively. H, I: Songs of the Red Fox Sparrow, whether from Newfoundland (H) or Copper River drainage in Alaska (I), consist mostly of pure whistles, and each male tends to have a single song form. H recorded in Quebec, 31 Jun 1989, from Elliott et al. 1997, I from Peyton 1999. Prepared on a Kay-Elementrics Co. DSP 5500 Sona-Graph, with transform size of 256 points (234 Hz).



Songs of Slate-colored birds also vary geographically. Birds in one canyon had especially distinctive songs (Martin 1979). As in Maritime Provinces, neighboring males also shared nearly identical song types. Among 62–71 birds in each year of Martin's study, and among total of 390 songs in their collective repertoires, only 5 major song types occurred, again revealing that males learn their songs from each other (only 15% of the 390 songs did not readily fit into these 5 common patterns).

Needed is a rangewide comparison of singing behavior for Fox Sparrow, to determine if tendency for a single song form is consistent across range of Red form and to document how all western populations organize their singing behavior (see also Fig. 4). The >400 samples of vocal behavior in Cornell University's Library of Natural Sounds would be a good place to start.

FEMALE SONG. Female occasionally sings, though more softly and briefly than male (Martin 1977). Saunders (1910: 80) described 2 birds singing alternately, as if rival males. Their songs were similar "in every way except that one was somewhat weaker than the other. I finally secured the bird with the weaker song and was much surprised when, on later examination, it proved to be a female." Blacquiere (1979) thought he recorded female song once, though the sex was unconfirmed.

CALLS. Calls described from Newfoundland by Blacquiere (1979), the first 4 in response to playback of male territorial song.

Check. About 20 ms, "an explosive aspirate" (Moore 1913: 179), "the usual alarm note, a loud 'smack'" (Townsend and Allen 1907: 403), a "thrasher-like *chuck* of alarm" (Linsdale 1928a: 274), midfrequency about 4 kHz. Given by males during territorial counters, by male and female when nest is approached by a human, and by male and sometimes female in response to song playback within territory (see below).

Sip. Also about 20 ms, a sharp note with midfrequency about 8 kHz, given only by "males in an apparent state of extreme agitation" (Blacquiere 1979: 27).

Chu-chu. Each *chu* note about 50 ms, extending from 3 to 7 kHz, several (7 in only example given) *chu* notes given in succession at rate of 4/s. Heard by Blacquiere only once, during song playback, by presumed female as male was singing nearby, the calling bird's head moving up and down. Probably same call described by Townsend and Allen (1907): "One individual who was 'smacking' in a fir tree emitted faint sneezy notes with motions of swallowing between the smacks" (Blacquiere 1979: 28). (L. Peyton [unpubl.] heard similar sounds from a male in which 2 large fly maggots had eaten away the nasal cavity.)

"Inter-song notes." Sometimes given just before song, an "unstructured series of syllable like notes," (Blacquiere 1979: 28) much like notes given between songs just after male arrives on breeding territory in spring.

Other calls. *Tsip.* A faint call heard in late summer, from small flock of 5 birds perched in dense vegetation. Probably same as "long drawn . . . *stssp* so commonly heard in Massachusetts during the migrations" (Linsdale 1928a: 285); also described by Townsend and Allen (1907) for migrating birds. Function unclear, but often given as birds are disturbed and rise to a higher perch. Two other notes reported by Terrill (1968: 1408): a modified "*tchek*" given by flock of migrating birds going to roost, and a "peculiar note, shrill, prolonged—a kind of squeal" from fighting birds in migration.

Geographic variation. "Common contact calls" (referred to above as *check* calls) vary geographically among Fox Sparrow groups (Garrett et al. 2000). In Red, Sooty, and Slate-colored groups, the call is "a smacking *tik* or *thick*," about 25 ms in duration, a "click-like *tik*" ranging from 3 to 10 kHz, a "burst of energy that terminates extremely quickly." Call of Thick-billed group, in contrast, is a *chink*, with a "metallic, whistle-like quality," about 50 ms, the energy concentrated in a narrow frequency band at about 5 kHz (Garrett et al. 2000: 412–413). See Garrett et al. 2000 for sonograms. Thorough rangewide comparison of calls needed, not only for *check* call but also for other calls, such as nestling begging *seep*; calls most likely not learned and would therefore provide better systematic information than would songs.

Phenology. Birds often sing in spring migration (e.g., Eaton 1914), seeming to improve as they approach breeding grounds, typically arriving there in full song (Townsend and Allen 1907, Terrill 1968). During migration, claimed to sing best in the evening (Saunders 1948). On breeding territory in early spring, Blacquiere (1979) recorded 4 or 5 males still in subsong, Martin (1977) only 1, and that one progressed to full song within 3 d.

In both Newfoundland and Utah/Idaho, birds sing vigorously shortly after their arrival on breeding grounds (early to mid-Apr in Newfoundland, late Mar through Apr in Utah/Idaho) until young hatch (Martin 1977, Blacquiere 1979). In Utah/Idaho, males sing little as they care for nestling and early fledglings (from third week of May until first week of Jun), but then sing more from mid-Jun until mid-Jul, when singing stops for breeding season (Martin 1977). Some resurgence of singing in early fall after postnuptial molt (Saunders 1948, Martin 1977).

Daily pattern. Has a reputation for lusty singing, on bright sunny days and in foul weather, from

"morn till late at night" (references in Linsdale 1928a: 28). Sings during dawn chorus, beginning "just after it began to get light prior to dawn," continuing 3–4 h, with reduced singing during midday and more frequent singing again near dusk (Blacquiere 1979: 36).

Places of vocalizing. "... [S]ings generally from a concealed perch inside of a spruce or fir tree a foot or two from the top..." (Townsend and Allen 1907: 402; see also Moore 1913). In Newfoundland, "2–3 song perches regularly used by the males, usually in the tallest trees in the territory, within one meter of the top and close to the trunk" (Blacquiere 1979: 36). For other vocalizations, see above.

Repertoire and delivery of songs. Song repertoire size differs among Fox Sparrow groups, from typically 1 song type in Red group (Maritime Provinces to Alaska) to 3 or 4 in Slate-colored group (Utah/Idaho; see above), perhaps even more in other groups, as evidenced by 1 Thick-billed male with 7 types (Fig. 4). If a male Red Fox Sparrow in Newfoundland has 2 songs, he alternates them, in A B A B A B format (Blacquiere 1979), though Red forms in Alaska with 2 types do not always alternate (L. Peyton unpubl.). Slate-colored males also tend to sing all of the songs in their repertoire before repeating them, such as A B A B for a 2-repertoire male, or A B C A B C, or A B C D A B C D for 3- and 4-repertoire males, such that all songs are used with about equal frequency. Sequences of songs rigidly adhered to, and a first-order Markov chain describes song sequencing habits of majority of males in Utah/Idaho population (e.g., 36 of 39 males with repertoires of ≥ 3 songs). See Figure 4 and Martin 1990 for more details.

Repertoire of syllable types for Slate-colored males correlated with song repertoire size. Males with 2, 3, and 4 song types had average of 16, 20, and 24 syllable types, respectively; range of syllable repertoires from 10 to 33. Total of 49 syllable types described all syllables in study population, all types present in both years, and 22 of the 49 were shared by more than half of the birds, again revealing the song similarity among the birds and that they learn from each other (Martin 1979).

Rate of singing up to 6 songs a minute during dawn chorus in Newfoundland (Blacquiere 1979), comparable to rate of singing in Utah/Idaho, where males average 7 s between songs (Martin 1990).

Songs in repertoire appear to have no functional difference, as males respond similarly to playback of all types (Martin 1980).

Social context and presumed functions. See above.

NONVOCAL SOUNDS

None reported.

BEHAVIOR

LOCOMOTION

Walking, hopping, etc. Little information. Typical undisturbed movement involves a hopping motion, in which both legs are moved in synchrony (Hailman 1973).

Flight. Seldom seen taking long flights (Gabrielson and Lincoln 1959). When disturbed, often flies close to ground, with a nervous, jerky flitting of tail (Gabrielson and Lincoln 1959).

SELF-MAINTENANCE

Preening, head-scratching, stretching, bathing, anting, etc. Twice, Hailman (1959) observed a recently banded and released Fox Sparrow use its bill to anoint its tarsi with preening oil. In both cases, bird continued to grasp perch with both feet and bent its head down to rub side of its bill from top of tarsus to toes (Hailman 1959).

Sleeping, roosting, sunbathing. During winter in Bloomington, IN, Fox Sparrows roosted overnight in thick red cedar (*Juniperus virginiana*) and yew (*Taxus* sp.) hedges, typically arriving at roost site at dusk (Rogers and Rogers 1990).

Daily time budget. No information.

AGONISTIC BEHAVIOR

Physical interactions. Little information. Blacquiere (1979) observed 3 sets of chases, each between 2 birds, which he assumed were territorial males in a boundary dispute. Once, Blacquiere (1979) observed a long sequence (approx. 10 min) of chases and singing involving various combinations of 3 birds. Typically, during this sequence, 1 Fox Sparrow sang 3 or 4 times from a perch 3 m above the ground and then flew at and chased one or both of the other birds, which were on the ground. Occasionally, nonsinging bird flew at singer. Eventually 1 individual flew off, leaving other 2 to continue sequence of singing and chasing. Chases consisted of fluttering and hopping on the ground or hopping between perches in dense undergrowth until nonsinger flew a short distance away, scratched and pecked at the ground while the singer sang again from a low perch.

Communicative interactions. No information.

SPACING

Territoriality. Territory size ranges from 0.25 to 1 ha in Newfoundland (Threlfall and Blacquiere 1982). Degree of territory fidelity once young are independent not known (Blacquiere 1979).

Birds establish territories within 1 d of arrival on breeding grounds (Blacquiere 1979).

Individual distance. No information.

SEXUAL BEHAVIOR

Mating system and sex ratio. No information.

Pair bond. Pairs form within a week of spring arrival, soon after males have established territories (Blacquiere 1979).

Little known about courtship. However, Blacquiere (1979) described one observation of courtship in Newfoundland. Male sang from an unusually low perch in underbrush 3 m from nest. Female flew in carrying several pieces of dead grass in her bill and perched about 1 m from the ground. Male, singing frequently, approached female within 0.5 m and began a wing-droop and wing-quiver display, which continued as he approached. When male mounted female, both individuals fluttered their wings, apparently to maintain balance on perch. During copulation, which lasted only 2–3 s, female dropped some grass she was carrying. After copulation, male repeated his wing-droop and quiver display 3 or 4 times while female flew down to retrieve fallen grass and flew into underbrush.

No information on duration or maintenance of pair bond.

Extra-pair copulations. No information.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. During winter and migration, sometimes travel in small groups (Bendire 1889). During late summer, Blacquiere (1979) noted seeing small groups of 2–6 Fox Sparrows, including fully grown immatures and adults. Outside breeding season, usually solitary or found in small groups; larger groups occasionally during migration (Byers et al. 1995).

Play. Not known.

Nonpredatory interspecific interactions. On migration, single birds or small groups occasionally found associating with White-crowned (*Zonotrichia leucophrys*) and Golden-crowned (*Z. atricapilla*) sparrows (Linsdale 1928a). Based on one observation of a Fox Sparrow singing in a tree with 2 singing Black-headed Grosbeaks (*Pheucticus melanocephalus*), Linsdale (1928a) suggested that Fox Sparrows are tolerant of other species on their territories. In another instance, however, a male drove a Western Tanager (*Piranga ludoviciana*) and a Gray Flycatcher (*Empidonax wrightii*) off of its territory (Linsdale 1928a).

PREDATION

Kinds of predators. Fox Sparrows make up 9% (13% by biomass) of prey taken by Merlins (*Falco columbarius*) breeding in Denali National Park, AK (Laing 1985). At nests other predators include Steller's Jays (*Cyanocitta stelleri*), and probably other predatory birds, mustelids, chipmunks, and snakes (Linsdale 1928a, Austin 1968).

Response to predators. Parents feign a broken wing and utter a metallic "chip" to decoy predators, including humans, away from nest (Pierce 1921, Rising 1987). Adults aggressive and frequently give a loud "check" call when nest is disturbed (Blacquiere 1979).

BREEDING

PHENOLOGY

Few data; see Figure 5. Approximate length of breeding period near Juneau, se. Alaska: 3 mo (Rogers 1994). Cloacal protuberance and brood patches present from Apr through Aug (Pyle 1997). Testes and ovaries enlarged and brood patch partially defeathered beginning as early as Apr (museum specimens LSUMNS, UWBM). Arrives on breeding grounds from early Apr through early May, often before snow has melted (see Migration, above; Philipp 1925).

Pair formation. In Newfoundland, most pairs arrived during first 2 wk of Apr; male establishes territory and, within a week after arrival, establishes a pair bond (Blacquiere 1979, Threlfall and Blacquiere 1982).

Nest-building. Nests of *P. i. schistacea* usually built in 2–3 d, but in one instance, a pair constructed an entire nest in 1 d and female laid first egg in nest that evening (Bendire 1889). Female puts final touches on nest, adding inner lining (Bendire 1889). Apparently, in *P. i. megarhyncha*, female is sole nest builder (Mailliard 1921).

First/only brood per season. EGG-LAYING. Few data; 2–5 eggs laid starting from early May through Jun and even into early Jul (Bendire 1889; Pierce 1921; Linsdale 1928a; Austin 1932, 1968; Terrill 1968; Threlfall and Blacquiere 1982; Peck and James 1987; Rogers 1994). In Newfoundland, onset of laying relatively constant from late Apr to mid-Jun, then drops off, with no laying after 5 Jul (Threlfall and Blacquiere 1982). For 10 wk, starting 27 Apr in Newfoundland, distribution of number of nests in which laying started was as follows: 6, 8, 2, 4, 7, 6, 7, 2, 1, 1. One egg laid/d (Pierce 1921, Ryan 1974).

HATCHING OF FIRST CHICKS. No data. However, given incubation period and egg-laying dates, occurs mid-May to late Jul.

DEPARTURE OF YOUNG FROM NEST OR CESSATION OF CLOSE PARENTAL CARE. In Newfoundland, some young have already fledged by 1 Jun (Terrill 1968). On west coast of James Bay, first fledglings seen 22 Jul; between 22 Jun and 3 Jul, on the north shore of the Gulf of St. Lawrence, many young fledged and being fed by parents, others no longer under parental care (Terrill 1968). Nestling period (hatching to departure from nest) approximately 10.5 d for

one nest at Bonavista, Newfoundland (Ryan 1974). For this same nest, time from laying of first egg to young leaving nest: 26 d (Ryan 1974).

Second/later broods per season. Little information; no records of double-brooding. However, long breeding period and observations of fresh eggs late in nesting season (late Jun), when many young have already fledged, suggest that *P. i. iliaca*, *P. i. schistacea*, and *P. i. townsendi* may lay second broods (Bendire 1889, Philipp 1925, Linsdale 1928a, Terrill 1968, Rogers 1994). In Newfoundland, no evidence of double-brooding (Threlfall and Blacquiere 1982). *P. i. fulva*, a member of the *megarhyncha* group, apparently rears only 1 brood/breeding season (Bendire 1889). Studies of color-marked birds needed.

NEST SITE

Selection. No information.

Microhabitat. Across entire range, nests on ground, in bushes, or even low trees (Bendire 1889, Harrison 1979, Austin 1968, Terrill 1968, Threlfall and Blacquiere 1982, Burns and Hackett 1993). In Newfoundland, commonly nests in or under coniferous trees or among the roots of upturned stumps (Linsdale 1928a, Terrill 1968, Threlfall and Blacquiere 1982). Of 2 ground nests recorded in Ontario: 1 at base of a moss (*Sphagnum* sp.) hummock, 1 under a small black spruce (Peck and James 1987). Of 6 *P. i. megarhyncha* nests found on ground, all were concealed by vegetation: Douglas fir (*Pseudotsuga menziesii*) seedlings ($n = 2$), a thicket of chinquapin (*Castanopsis* sp.; $n = 1$), leaning limb of an oak (*Quercus* sp.; $n = 1$), deer brush (*Ceanothus* sp.; $n = 1$), and a piece of lodged bark ($n = 1$; Mailliard 1921). Of 14 ground nests found in Fresno Co., CA, by Burns and Hackett (1993), however, none was located under conifers.

Nests built in trees or bushes often placed in crotches, elbows, or other such supports (Terrill 1968). Of several nests described from e. Canada, 1 was built on a dead branch leaning against a small spruce, 2 were in the elbows of deformed white spruce (*Picea glauca*), and one was in the crotch of a yellow birch (*Betula alleghaniensis*; Terrill 1968). At Lake Tahoe, CA, 3 of 14 *P. i. megarhyncha* nests were in deer brush in or on edge of a thicket; 1 was in a crotch formed by a 5-cm shoot and the main trunk of a willow; 1 was in a mass of dead branches and debris under a willow clump; and 1 was on a dead aspen (*Populus* spp.) branch over a small stream (Mailliard 1921). Regardless of where nests are built, they are usually well concealed (Austin 1968, Burns and Hackett 1993). In Sequoia National Forest, 7.5 km west of Hume, Fresno Co., CA (boundary between *P. i. stephensi* and *P. i. megarhyncha*), of 23 Fox Sparrow nests found, 40% were completely concealed, 32% were only 25% visible, 12% were

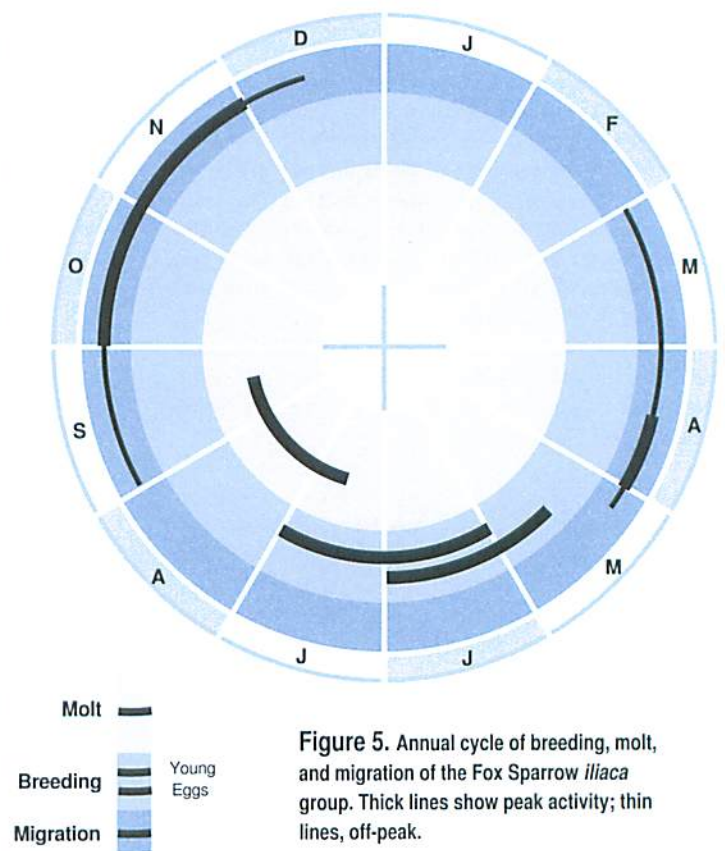


Figure 5. Annual cycle of breeding, molt, and migration of the Fox Sparrow *iliaca* group. Thick lines show peak activity; thin lines, off-peak.

50% visible, and 16% were completely visible without moving any branches (Burns and Hackett 1993). On average, these nests were placed 85 cm from nearest edge of nest plant and 84 cm from top of nest plant (Burns and Hackett 1993).

Site characteristics. Some specific nest heights from Canada: 1 at 0.6 m, 2 at 1.5 m (Austin 1968), and 1 at 1.8 m above ground (Ryan 1974). Nests also found much higher, including some as high as 6 m (Philipp 1925, Linsdale 1928a, Terrill 1968, Threlfall and Blacquiere 1982). In St. John's, Newfoundland, 1 of 46 nests was 6 m off the ground, 45 were ≤ 2.7 m; of these 45, 24 (53%) in trees, 21 (47%) on the ground (Threlfall and Blacquiere 1982). Later nests significantly lower to ground than earlier ones, a change that may be related to snow cover (Philipp 1925, Threlfall and Blacquiere 1982). Some specific nest heights from Hume, Fresno Co., CA (near boundary of *P. i. stephensi* and *P. i. megarhyncha*): 14 out of 23 nests (61%) placed on the ground, mean height of above-ground nests ($n = 9$) 30 cm \pm 10.8 SD, mean height of nest plants 1.41 m \pm 0.66 SD (Burns and Hackett 1993).

Nest placement within habitat varies geographically. In Newfoundland, most nests were placed under conifers; Fox Sparrows from Gull I., Newfoundland, nested in a climax forest of balsam fir,

black spruce, and white spruce (Threlfall and Blacquiére 1982). In Hume, Fresno Co., CA, however, no nests were placed in or under conifers (Burns and Hackett 1993).

Nest-site habitat characteristics of Fox Sparrows in w. North America are quite different from those in the East. Preferred nest sites consist of chaparral with dense shrubby vegetation for concealment (Burns and Hackett 1993; see Habitat: breeding range, above). Rather than choosing nest sites based on species of plants present, it appears that Fox Sparrows focus on more general habitat characteristics such as presence of dense shrubby vegetation for concealment of nests from predators (Burns and Hackett 1993).

NEST

Construction. Little information, but female appears likely to construct the nest alone (Mailliard 1921, Burns 1988). Two to 3 d needed to construct a nest, but in one instance, a pair built an entirely new nest between sunrise and sunset of the same day (Bendire 1889).

Structure and composition matter. From Bendire 1889, Philipp 1925, Terrill 1968, Ryan 1974, Threlfall 1979, Threlfall and Blacquiére 1982, and others as noted. Nests of northern and eastern *iliaca* group composed of a wide variety of materials. Outer wall or rim of nest constructed from small twigs (often black spruce or balsam fir), shredded wood, rotting wood, broom moss (*Dicranum* sp.), strips of bark (sometimes dry and scaly), coarse dry grasses, mosses (*Polystichum* sp. and *Sphagnum* sp.), lichens (*Alectoria* sp. and *Usnea* sp.), and reindeer moss (*Cladonia rangifera*). Inner cup or nest lining composed of an assortment of materials including fine dead grass, rootlets, hair (from sheep [*Ovis aries*], cow [*Bos taurus*], dog [*Canis familiaris*]), feathers, lichens (*Alectoria* sp.), moss, and monofilament fishing line. Nest composition and structure varies with nest placement: Tree nests bulkier and heavier (mean mass 49.6 g [range 39.0–59.7, $n = 5$]) than ground nests (mass 9.8 g, 15.2 g [$n = 2$]; Threlfall 1979, Threlfall and Blacquiére 1982). Nests in trees have outer wall of black-spruce twigs, rotting wood, lichens, and moss with inner cup of dead grass. Ground nests built from dead grasses are set into a depression that supports sides of nest. Inner linings of ground and tree nests similar.

In w. North America, members of the *schistacea*, *megarhyncha*, and *unalaschensis* groups construct nests from materials similar to those used by members of the *iliaca* group (Bendire 1889, Grinnell 1910, Mailliard 1921, Austin 1968, Harrison 1979, Burns and Hackett 1993).

Dimensions. A nest from Moose Factory, Ontario (U.S. National Museum 4411) measured 12.7 cm

wide \times 7.62 cm deep on outside and 7.62 cm wide \times 5.08 cm deep on inside (Bendire 1889). In Fresno Co., CA (boundary between *P. i. stephensi* and *P. i. megarhyncha*): mean of outside diameter 6.9 cm \pm 1.2 SD; outside height 6.7 cm \pm 1.2 SD; depth 4.8 cm \pm 0.9 SD ($n = 23$; Burns and Hackett 1993). Nest size varies regionally, but pattern is unclear. Nest dimensions from other localities include: San Bernardino Mtns., CA (*P. i. stephensi*; average in cm, $n = 4$), outside diameter 15.2, inside diameter 7.6, outside depth 11.4, inside depth 4.4 (Pierce 1921); Lake Tahoe, CA (*P. i. megarhyncha*; range in cm, $n = 14$), outside diameter 15.2–35.5, inside diameter 6.3–7.6, outside depth 7.6–13.9, and inside depth 2.5–4.4 (Mailliard 1921).

Microclimate. No data.

Nonbreeding nests. Before first clutch is laid, may build >1 nest (Threlfall and Blacquiére 1982). Will abandon first nest and build a second to renest if first clutch is destroyed (Threlfall 1979, Burns 1988).

EGGS

Shape. Oval (Grinnell 1910, Harrison 1979).

Size. Mean length and breadth, in mm: *iliaca* from Newfoundland, 23.5 ± 0.84 SD \times 17.1 ± 0.50 SD ($n = 20$; Threlfall and Blacquiére 1982); *stephensi*, 22.08 ± 1.08 SD \times 17.06 ± 0.86 SD ($n = 17$; Pierce 1921). A lack of published egg-measurement data including standard deviations makes assessing patterns of geographic variation in egg size difficult.

Mass. Mean mass of *P. i. iliaca* eggs from Newfoundland: 3.5 g \pm 0.20 SD ($n = 21$; Threlfall and Blacquiére 1982), about 10% of female body mass.

Color. Slightly glossy; pale bluish green, boldly marked with spots, blotches, cloudings of reddish brown; considerable variation in pattern and color (Pierce 1921, Harrison 1979). Ground color occasionally obscured by brownish markings (Bendire 1889). In Newfoundland, brown spotting tends to be concentrated on larger end of egg (Blacquiére 1979).

Surface texture. Slightly glossy when laid, but gloss fades with time (Blacquiére 1979).

Eggshell thickness. No information.

Clutch size. Mean clutch size in Newfoundland: 3.24 ± 0.60 SD (range 2–4 [$n = 34$]; Threlfall and Blacquiére 1982). Two out of 50 *P. i. schistacea* nests examined by Bendire (1889) had 5 eggs. Mean clutch size for *P. i. townsendi*, near Juneau, AK: 4.11 ± 0.33 SD ($n = 9$; Rogers 1994).

Egg-laying. Begins immediately after nest is complete (Threlfall and Blacquiére 1982). Eggs typically laid 1/d, early in morning (Blacquiére 1979).

INCUBATION

Onset of broodiness and incubation in relation to laying. No evidence of incubation before third,

and final, egg laid in one nest observed near Bonavista, Newfoundland (Ryan 1974). Threlfall and Blacquiere (1982), however, collected data from 8 nests and noted that at least 1 female started to incubate before clutch was complete. Incubation by female *P. i. megarhyncha* also begins as soon as first egg is laid (Mailliard 1921).

Incubation patch. Only female develops a brood patch, Apr–Aug (Pyle 1997).

Incubation period. About 12–14 d (Bendire 1889; Austin 1932, 1968; Terrill 1968; Blacquiere 1979; Harrison 1979). Range roughly equal for all 4 groups of Fox Sparrows. In Newfoundland, incubation period for 1 clutch: 12 d 4 h (Threlfall and Blacquiere 1982); 14 d for 3 nests studied near Bonavista, Newfoundland (Ryan 1974).

Parental behavior. In Newfoundland, incubation performed solely by female (Philipp 1925, Threlfall and Blacquiere 1982). In Hume, Fresno Co., CA, Burns (1988) observed only nonsinging birds, which he assumed to be female, incubating. Most likely for other populations, females are also sole incubators (Mailliard 1921, Austin 1968).

HATCHING

Preliminary events and vocalizations; shell-breaking and emergence. Details in Blacquiere 1979. Small area of shell is cracked and pipped. Once opening exists, chick makes weak vocalizations. Using egg tooth, breaks egg in a narrow line around larger end, near equator. Eventually, top of egg breaks off and chick emerges. Hatching relatively synchronous, all eggs hatching within 35 h of one another (Threlfall and Blacquiere 1982).

Parental assistance and disposal of eggshells. No eggshells found in nests with newly hatched nestlings, suggesting parents dispose of eggshells quickly (Blacquiere 1979).

YOUNG BIRDS

Condition at hatching. *P. i. megarhyncha*, at about 3 d old are helpless and downy (Austin 1968). *P. i. iliaca*, from Newfoundland, hatch out with a proportionately larger tarsus than Hume, CA, birds (Burns 1993). Plumage at hatching (natal down) not described (Terrill 1968).

Hatchling mean mass: *P. i. iliaca*, from Newfoundland, 3.2 g ($n = 4$; Blacquiere 1979); Hume, CA (where *P. i. stephensi* and *P. i. megarhyncha* meet), 2.4 g ($n = 4$; Burns 1993).

Growth and development. From Burns 1993 and others as noted. Nestlings grow rapidly (growth constant $k = 0.57$), with differential growth of particular morphological features favoring early development of legs and feet (Blacquiere 1979). Relative growth of tarsus length in relation to body mass is allometric; changes throughout development.

Comparing populations in Newfoundland (*P. i. iliaca*) and Hume, CA (where *P. i. stephensi* and *P. i. megarhyncha* meet), relative growth rates differ early in development, but eventually converge (see Burns 1993 for details). By the time young leave nest, they are well feathered (Terrill 1968). Juvenal plumage apparently acquired by a complete postnatal molt and resembles a first-winter plumage, but is browner with paler edgings, more streaks above, and heavier dusky streaks below (Dwight 1900; see Appearance, below).

PARENTAL CARE

Brooding. Nestlings apparently brooded only by female (Blacquiere 1979, Threlfall and Blacquiere 1982).

Feeding. Female apparently does most feeding of nestlings, but males recorded occasionally carrying food to young (Philipp 1925, Austin 1968, Terrill 1968, Blacquiere 1979, Burns 1988). Males also recorded passing food items to female, who then feeds them to nestlings (Grinnell et al. 1930, Austin 1968). Male recorded feeding one of its young 21 d after offspring fledged (Blacquiere 1979).

Young fed at intervals of 2–5 min (Linsdale 1928a). Parent gathers food from forest-floor litter. Grinnell et al. (1930) observed and collected several adults gathering insect food for young, including one individual that carried 2 large ants and a caterpillar in its bill. Nestlings probably fed primarily animal matter (Linsdale 1928a, Blacquiere 1979). See Food habits: diet, above, for further details.

Nest sanitation. Parents keep nest “scrupulously clean” (Philipp 1925). Female eats fecal sacs of her nestlings as sacs are voided (Linsdale 1928a, Grinnell et al. 1930).

COOPERATIVE BREEDING

No information.

BROOD PARASITISM

Identity of parasitic species. Infrequently parasitized by Brown-headed Cowbirds (*Molothrus ater*; Friedmann 1963). Brown-headed Cowbird eggs and young found in nests of several Fox Sparrow subspecies, including *zaboria*, *olivacea*, *schistacea*, *swarthi*, *fulva*, and *monoensis* (Bendire 1889, Austin 1968).

Frequency of occurrence, seasonal or geographic variation. Although Brown-headed Cowbirds were common in Fresno Co., CA, Burns (1988) did not find any cowbird eggs or young in Fox Sparrow nests ($n = 23$). No cowbird eggs found in 9 *P. i. townsendi* nests observed throughout breeding season near Juneau, AK (Rogers 1994). In the East, Fox Sparrow not parasitized by Brown-headed Cowbirds because ranges do not overlap (Terrill 1968).

Timing of laying in relation to host's laying. No information.

Response to parasitic mother, eggs, or nestlings. No information.

Effects of parasitism on host. No information.

Success of parasite with this host. No information.

FLEDGLING STAGE

Departure from nest. As early as beginning of Jun (Todd 1963, Austin 1968, Terrill 1968). Near Juneau, AK, last nestling fledged by 2 Jul (Rogers 1994).

AGE AT DEPARTURE. Nine to 10.5 d between hatching of young and departure from nest (Ryan, 1974, Blacquiere 1979).

CONDITION OF DEVELOPMENT AT DEPARTURE. In some cases, fledglings unable to fly (Blacquiere 1979).

MANNER OF DEPARTURE. When young nearly ready to leave nest, they jump out and hop away (Blacquiere 1979).

Growth. From Blacquiere 1979. Nestling body mass at fledging: 25–26 g (about 64% of adult mass). Of 8 body parameters measured in *P. i. iliaca* from Newfoundland, only tarsus reached full adult size prior to fledging. At fledging, measurement of length of hallux plus claw was 83% of adult size; all other body parameters <75% of adult size.

Association with parents or other young. Once young leave nest, they are accompanied by parents; one color-banded adult male *P. i. iliaca*, still on its territory 21 d after its nestlings fledged, fed one of its fledglings (Blacquiere 1979). In Aug, family groups observed with fully fledged young (Austin 1968).

Ability to get around, feed, and care for self. No information.

IMMATURE STAGE

In comparison to other passerines, skulls of Fox Sparrows pneumatize slowly (Stewart 1972). Skull pneumatization completes as early as 1 Dec, but some second-year birds may retain unpneumatized 'windows' on top of the skull through summer and rarely into fall (Pyle 1997). In most cases, window in skull retained longer than the Bursa of Fabricius (LSUMNS, UWBM). In one case, however, a bird with a completely ossified skull and a 6 × 4-mm granular ovary had a 5 × 4-mm bursa (UWBM).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. No information.

Clutch. See Breeding: eggs, above.

Annual and lifetime reproductive success. No information on lifetime reproductive success. For Fox Sparrows from Sheep Creek Valley near Juneau, se. Alaska, apparent nest success = 0.632 and Mayfield nest success = 0.573 ($n = 19$; Rogers 1994). At same location, fledglings/nest = 1.96 and fledglings/successful (hatching ≥ 1 young) nest = 3.38 (Rogers 1994). Of these nests, 36.8% ($n = 9$) failed to hatch eggs, with 31.6% failing from predation and 5.2% failing from other causes (Rogers 1994).

Number of broods normally reared per season. Few data; generally 1/yr.

Proportion of total females that rear at least one brood to nest-leaving or independence. From Sheep Creek Valley near Juneau, 63.2% ($n = 19$) of Fox Sparrow nests fledged ≥ 1 young (Rogers 1994).

LIFE SPAN AND SURVIVORSHIP

Estimated longevity of Fox Sparrows wintering at Coyote Creek, CA, is 6 yr 7 mo (Sandercock and Jaramillo 2002). At same location, annual probability of local survival is $10.8\% \pm 1.2$ SE for immatures after first capture, $27.4\% \pm 8.1$ SE for adults after first capture, and $35.2\% \pm 0.0$ SE for adults in later years. Recapture probabilities, which provide an index of survival, were $0.603\% \pm 0.065$ SE for immatures and $0.496\% \pm 0.086$ SE for adults at this same location (Sandercock and Jaramillo 2002). Longevity record for a Fox Sparrow is 9 yr 9 mo (Kennard 1975).

DISEASE AND BODY PARASITES

Diseases. No information.

Body parasites. From Jewer and Threlfall (1978), who found that all Fox Sparrows they examined ($n = 20$) from Newfoundland had parasites. Known to host 20 genera of parasites, including 10 helminths, 8 arthropod ectoparasites, and 2 haematozoans. Most lightly infected bird was an AHY female that carried a moderate infection of *Haemoproteus fringillae* and *Haemoproteus orizivora*; 18 of 20 (90%) Fox Sparrows sampled were parasitized by helminths (5 genera of Trematoda [*Conspicuum*, *Brachylecithum*, *Zonorchis*, *Tanaisia*, shistosomid sp.], 2 genera of Cestoda [*Paricterotaenia*, *Aploparaksis*], 3 genera of Nematoda [*Syngamus*, *Capillaria*, *Porrocaecum*]) and 19 of 20 (95%) Fox Sparrows sampled carried ectoparasites (4 genera of Pthiraptera [*Philoapterus*, *Myrsidea*, *Ricinus*, *Brueelia*], 1 genus of Siphonaptera [*Ceratophyllus*], 3 genera of Acarina [*Haemaphysalis*, *Proctophyllodes*, *Analges*]). Six out of 19 (32%) birds from which blood smears were taken bore Haematozoa of 2 genera (*Leucocytozoon*, *Haemoproteus*). See Jewer and Threlfall 1978 for details; see also Table 1.

Table 1. Parasites found on 20 Fox Sparrows in Newfoundland.*

Parasites	Prevalence Number of birds (%) infected	Intensity/infected bird		Location in/on bird ¹	Classification
		Mean number	Range of numbers		
<i>Conspicuum icteridorum</i>	3 (15)	3	1-7	2, 3, 4	Trematoda
<i>Brachylecithum stunkardi</i>	4 (25)	4	1-7+	4	Trematoda
<i>Zonorchis alveyi</i>	1 (5)	1	1	5	Trematoda
<i>Tanaisia zarudnyi</i>	4 (25)	2	1-2	6	Trematoda
Shistosomid	1 (5)	1	1	8	Trematoda
<i>Paricterotaenia passerellae</i>	6 (30)	10	1-28	2, 3a	Cestoda
<i>Aploparaksis elisae</i>	9 (45)	4	1-13	2, 3	Cestoda
<i>Syngamus trachea</i>	4 (25)	3	2-4	7	Nematoda
<i>Capillaria contorta</i>	3 (15)	3	1-7	1	Nematoda
<i>Porrocaecum brevispiculum</i>	1 (5)	1	1	3b	Nematoda
<i>Philopterus fringillae</i>	10 (50)	19	1-62	9, 12, 13, 14	Pthiraptera
<i>Myrsidae incerta</i>	9 (45)	4	1-9	9, 12, 13	Pthiraptera
<i>Ricinius fringillae</i>	2 (10)	8	7-8	10, 12, 14	Pthiraptera
<i>Brueelia vulgata</i>	2 (10)	5	2-7	10, 11	Pthiraptera
<i>Ceratophyllus garei</i>	4 (20)	1	1	9	Siphonaptera
<i>Haemaphysalis leporispalustris</i>	1 (5)	1	1	14	Acarina
<i>Proctophyllodes</i> sp.	12 (60)	61	5-250	12	Acarina
<i>Analges</i> sp.	1 (5)	4	4	10, 13	Acarina

*Table modified from Jewer and Threlfall 1978.

¹1 = esophagus; 2 = duodenum; 3 = small intestine (a) anterior (b) mid; 4 = bile ducts; 5 = gall bladder; 6 = kidneys; 7 = trachea; 8 = blood vessel; 9 = body; 10 = back; 11 = breast; 12 = wings; 13 = neck; 14 = head.

CAUSES OF MORTALITY

Inclement weather, especially freezing rain and deep snow, during spring migration and on wintering grounds, can cause high mortality (Terrill 1968). A population of Fox Sparrows wintering on Mandarte I., British Columbia, declined 63% during a period of severe winter weather; mortality (vs. dispersal) probably played a role here (Rogers et al. 1991).

Five out of 16 *P. i. megarhyncha* nests found by A. M. Ingersoll had pipped eggs or nestlings killed by Steller's Jays (Austin 1968). In Hume, Fresno Co., CA, 50% of nests revisited by Burns (1988) were depredated. Fox Sparrows respond to such depredation, however, by quickly renesting (Blacquiere 1979, Threlfall and Blacquiere 1982, Burns 1988).

RANGE

Initial dispersal from natal site. No information.

Fidelity to breeding site and winter home range. Twelve (23%) of 51 birds banded in 1970 on Gull I., Newfoundland, were recaptured on the island in 1971 (Threlfall and Blacquiere 1982). Nine (75%) of these were recaptured in nets set in same place each year, and remaining 3 (25%) were recaptured within 50 m of their banding location (Threlfall and Blacquiere 1982).

Dispersal from breeding site or colony. No information.

Home range. No information.

POPULATION STATUS

Numbers. On Breeding Bird Survey (BBS) routes in w. U.S., anywhere from <5 to 50 individuals detected/route/yr (Price et al. 1995). In e. U.S., numbers detected/route/yr lower, <5-20 (Price et al. 1995). Density of breeding pairs varies among localities; most likely depends on habitat productivity (Blacquiere 1979). In n. Ontario, 15 of 32 10-km squares had >10 pairs/square (Rising 1987). In Jackson Hole, WY, density estimated at 2 individuals/4.5 ha. In Mineral, CA, 6 breeding pairs/2.63 ha (Linsdale 1928a). In some places in Alberta, densities as high as 12 pairs/1.61 km² (Linsdale 1928a). In Sierra Nevada, peak densities of about 1 pair/ha (Zink 1986).

Winter abundance highest along rivers; e.g., near Red River along border between Texas and Oklahoma (Root 1988). Winter abundance peaks also along Pacific and Atlantic coasts and along Mississippi and Tennessee Rivers, with lower relative abundance along Colorado and Missouri Rivers (Root 1988). In 1971, at Monte Vista National Wildlife Refuge, Alamosa, CO, 80 Fox Sparrows

were recorded on Christmas Bird Counts, leading to an ephemeral peak in abundance for that location (Root 1988).

Trends. From 1966 to 1979, BBS data show a significant ($p < 0.01$) positive rate of annual change (30.8%) of Fox Sparrows in Newfoundland. No other location shows statistically significant trends for this time period and this trend not found in BBS data from Newfoundland for other time periods. Between 1925 and 1940 at Fox Bay, Magdalen Is., Quebec, abundance went from "common everywhere" (Philipp 1925) to only 6 found (Braund and McCullagh 1940).

POPULATION REGULATION

No information.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

No information. Human disturbance does not appear to have a negative impact. For the most part, Fox Sparrows nest in areas not heavily affected by humans. However, human-induced logging and forest fires may affect distribution and abundance (see Distribution: historical changes and Habitat: breeding range, above).

MANAGEMENT

Other than habitat protection, no measures for management applied or suggested.

APPEARANCE

MOLTS AND PLUMAGES

See Figure 5. The following descriptions based on Cramp and Perrins 1994, for *P. i. iliaca*, unless otherwise noted. Dwight's (1900) description of molt also refers to *P. i. iliaca*. However, Pyle's (1997) description of molt applies generally to all Fox Sparrow subspecies. Sexes are alike in appearance, although female may average duller in coloration (Dwight 1900).

Hatchlings. J. M. Linsdale described 2 young of *P. i. megarhyncha*, thought to be about 3 d old, as helpless and downy rather than feathery (Grinnell et al. 1930). Hatchlings apparently otherwise undescribed.

Juvenal plumage. Juvenal plumage similar to Definitive Basic (adult) plumage, but body-feathers looser and softer in texture (Cramp and Perrins 1994), upperparts average duller, and underparts with buffy wash (Pyle 1997). In *P. i. unalaschcensis*, Dwight (1900) noted that Juvenal plumage resembled Basic I plumage but was "brownier with

paler edgings and more streaks above, and darker with heavier dusky streaking below" (Dwight 1900: 206). As in other passerines, outer Juvenal rectrices average more tapered than those of adults, and outer Juvenal primary-coverts somewhat narrower and more tapered than those of adults, and with narrower pale edges (Pyle 1997).

Basic I plumage. Prebasic I molt partial; includes all median and greater wing-coverts (rarely 1 or 2 outer greater-coverts retained), usually does not include any tertials or rectrices; molt occurs on breeding grounds Jul through Sep (Dwight 1900, Pyle 1997). Basic I plumage indistinguishable from Definitive Basic plumage except for presence of retained Juvenal feathers on wings and tail, which appear more worn by spring (Dwight 1900).

Alternate I plumage. As in Definitive Prealternate molt, Prealternate I molt, when present, limited to some head-feathers (Dwight 1900, Swarth 1920, Pyle 1997). Alternate I plumage similar to Basic I plumage, but retained Juvenal feathers may appear more worn (Pyle 1997).

Definitive Basic plumage. Definitive Prebasic molt complete (Dwight 1900), primaries replaced in order from P1 to P9 (Cramp and Perrins 1994); molt occurs on breeding grounds from Jul through Sep (Cramp and Perrins 1994, Pyle 1997).

Definitive Basic plumage practically indistinguishable from Basic I plumage (Dwight 1900). However, AHY/after second year (ASY) birds have truncate rectrices that are unworn relative to HY/second year (SY) birds (Pyle et al. 1987). From Sep to Apr, Fox Sparrows exhibit this fresh plumage, with cap, hindneck, upper side of neck, and upper mantle medium gray with each feather tipped broad, deep rufous-chestnut. These rufous-chestnut feather tips usually partly or largely conceal gray, except for gray stripe above eye. Scapulars and lower mantle are colored deep rufous-chestnut, with sides of these feathers fringed light olive-brown or buff-brown and sometimes partially mottled rufous-chestnut contrasting with bright cinnamon-rufous or fox-red upper tail-coverts. On freshly molted feathers, tips of tail-coverts narrowly fringed pale gray buff. Lore and eye-ring mottled off-white, dull gray, and occasionally rufous eventually merging into a finely streaked off-white and rich rufous-chestnut upper cheek and shorter ear-coverts. Sometimes exhibits a short, uniform, pale-buff or off-white stripe above lore. Lower cheek and longer ear-coverts rich rufous-chestnut, often with some pale-olive or gray feather bases visible on central ear-coverts. Chestnut coloration of lower cheek broken into 2 stripes by a short off-white stripe (usually speckled chestnut) backward from side of lower mandible. One of these chestnut stripes extends back from bill commissure and other

extends back from lower corner of lower mandible. White feather bases partially visible on lower side of rufous-chestnut neck. Underparts ground color pale cream to white, tinged cream-buff on lower flanks, thighs, and under tail-coverts. Chin and throat either uniform or speckled rich rufous-chestnut (occasionally joining to form a narrow band across upper throat). Breast and flanks have coarse, broad, triangular rufous-chestnut dots, sometimes coalescing into a band across breast. Chestnut marks on flanks more elongate, while upper belly and side of belly have smaller fuscous-brown or dull-black triangles. Tail deep rufous-cinnamon, with inner webs tinged brown or sooty. Remiges, greater upper primary-coverts, and alula are grayish black with an ill-defined narrow rufous-cinnamon fringe on outer web. This fringe absent from longest feather of alula. However, fringe of P9 and emarginated parts of P5–P8 are pale cinnamon to isabelline white. Lesser upper wing-coverts gray or olive-gray and suffused with a variable amount of rufous while median and greater upper wing-coverts and tertials grayish black with a broad rufous-chestnut outer fringe. Black is largely concealed, except on tertials. Median and greater wing-coverts have pale-buff to off-white spots on tips of outer webs, forming narrow broken wing-bar. Under wing-coverts and axillaries pale gray to off-white, with partial dull-gray variegation.

Definitive Alternate plumage. Definitive Pre-alternate molt, when present, is limited to some head-feathers (Dwight 1900, Swarth 1920, Pyle 1997); occurring Mar through Apr (Pyle 1997).

Definitive Alternate plumage similar to Definitive Basic plumage except for subtle differences due mainly to wear and fading. From roughly May through Jul, rufous-chestnut feather-tips of Definitive Basic plumage, which are found from cap to upper mantle, are partly or fully worn. Plumage from cap to upper mantle mainly gray with traces of chestnut spots or brown suffusion, especially on crown. Amount of chestnut and gray on cap and neck is individually variable, in part due to individual differences in abrasion and in part due to geographic origin. Birds from the East (e.g., Nova Scotia) tend to have more extensive chestnut and rufous tones, while farther west (e.g., Wisconsin), birds are grayer. Scapulars and lower mantle olive-brown to grayish with deep rufous-chestnut streaks. White stripe backward from lower mandible and pale olive-gray center to ear-coverts often more distinct than in Definitive Basic plumage, and there is usually a prominent white bar at lower rear of ear-coverts. Triangular rufous spots on underparts narrower and smaller and tend to coalesce less than in Definitive Basic plumage. Lower flanks and under tail-coverts have a cream-white ground color, with

spots on tips of median and greater upper wing-coverts whiter, but sometimes worn off.

BARE PARTS

Bill and gape. Bill grayish brown, dusky brown, dark plumbeous gray, or grayish black with basal half of lower mandible yellow, orange-flesh, yellow-orange, bright orange, or pinkish gray (Cramp and Perrins 1994). Data from recent specimens of various subspecies indicate that upper mandible coloration is dark horn, blackish horn, or blackish brown with pale (yellow or orange) edges (ramus, gape, and base; LSUMNS). However, lower mandible coloration greenish yellow, dull orange-yellow, dull yellow, or blue-gray (LSUMNS). On many specimens, pale lower mandible coloration blends and becomes darker toward dark bill-tip (LSUMNS). Presence or absence and intensity of yellow or orange coloration at base of mandible variable among populations, and is possibly seasonally variable (Garrett et al. 2000). While most Sooty Fox Sparrow populations have a rich orangish or yellowish base to mandible, Thick-billed Fox Sparrows have a grayish or gray-green base (Garrett et al. 2000). Soft-part colors also vary with age. At Hume, Fresno Co., CA, younger nestlings had gray-yellow upper mandible and yellow lower mandible, while older nestlings had entire bill pink, pink-brown, or occasionally gray-brown, with a yellow gape (LSUMNS). Fledglings had gray-brown or light-brown bill with yellow gape (LSUMNS).

Iris. Dark brown or red-brown, independent of age or sex (LSUMNS, UWBM).

Legs and feet. Dull flesh-gray, purplish brown-gray, brownish pink, light brown, dark brown, horn brown, or dark horn brown (Cramp and Perrins 1994, LSUMNS). Nestlings and fledglings from Hume, Fresno Co., CA (boundary between *stephensi* and *megarhyncha*) apparently have yellow, pink, or pinkish-brown legs and feet, with some birds showing pink coloration above and yellow below (LSUMNS).

MEASUREMENTS

LINEAR

See Appendix. Swarth (1920) gives mean values and ranges for samples of males of w. North America subspecies. Pyle (1997) gives ranges (without means or standard deviations) for males and females of most subspecies. Females slightly smaller than males: about 2–4 mm in wing-chord, 1–3 mm in tail, about 0.5 mm in bill (see Ridgway 1901, Rising 1996, Pyle 1997). *P. i. iliaca* males and females differ significantly in measurements of wing and tail (Cramp and Perrins 1994).

Within the *iliaca* group, populations vary clinally with northernmost populations (in Alaska) largest. Within *unalaschcensis* group, populations in Aleutians and sw. Alaska larger bodied and larger billed than those south of Yakutat Bay, AK (Swarth 1920, Rising 1996). Within *schistacea* group, measures of size (wing-chord, bill width, tarsus; also skeletal elements and mass) increase from *P. i. schistacea* populations of ne. Nevada to populations of *P. i. canescens* and *P. i. swarthi* of n. Utah (Swarth 1920, Zink 1986). *Megarhyncha* group also shows a north-to-south cline of increasing bill size (Swarth 1920, Zink and Kessen 1999).

MASS

See Appendix. For Alameda Co., CA, during non-breeding season, mean mass 32.4 g (range 21.7–42.1, $n = 221$ measures of 91 individuals of both sexes over period Sep 1932–May 1933); on average, mass increases from midmorning to evening; monthly means show a peak for Dec (34.0 g) and a premigration increase in Apr and May (35.6 g; Linsdale and Sumner 1934). For migrants in Pennsylvania, mean 36.9 g (range 29.6–49.0 [$n = 446$]; Clench and Leberman 1978). For spring and fall migrants in Cook, Co., IL, male mean 36.1 g \pm 2.5 SD (range 24.9–44.9, $n = 526$), female mean 33.9 g \pm 2.4 SD (range 25.3–45.7, $n = 466$; Field Museum of Natural History data from collision mortality).

OTHER

ONTOGENY

Burns (1988, 1993) found that geographic variation, exemplified by Red Fox Sparrow and Thick-billed Fox Sparrow, results from both different relative growth rates and relative timing of onset and offset of growth. Bill and tarsus length differ in relative growth rates, while wing and tail length differ in timing of onset of a similar growth rate (Burns 1988, 1993). Therefore, differences in adult morphology of different Fox Sparrow populations are reached via repatterning of developmental trajectories (Burns 1993).

TEMPORAL VARIATION IN MORPHOLOGY AND ALLOZYMES

Zink (1983) and (Burns and Zink 1990) assessed levels of temporal variation in morphology and allozymes. Across 50 yr for 7 populations, most morphological characters showed no significant differences; however, an average of 2.2 (7.1%) significant character differences was observed in these populations (Zink 1983). Multivariate analysis revealed these significant differences in only 2 of 7 sites. Burns and Zink (1990) found no temporal change in allozymic variation over 8–10 generations.

PRIORITIES FOR FUTURE RESEARCH

Relatively little is known about this species, given its abundance. There is still a need for descriptive work: Further studies of nesting behavior, using color-marked individuals, will help us to understand male and female roles, from nest-building to feeding fledged offspring. Most of the information on breeding biology comes from older publications, where researchers watched unmarked birds. Comparative evolutionary studies on migratory physiology and further studies on vocal evolution should prove fruitful. Finally, although the Fox Sparrow has been the focus of many phylogenetic and population genetic studies, there continues to be a need for more work in these areas. Finer-scale studies of population genetics, looking at contact/hybrid zones between named subspecies, could help further our understanding of the levels of genetic isolation between the 4 main Fox Sparrow lineages.

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Appendix. Linear measurements (mm) of representative samples of Fox Sparrows, males only. Data shown as mean (range); consolidated from subspecies samples in Swarth 1920. Mass (g) data as mean (range, *n*) for breeding adults only, sexes pooled (LSUMNS, MMNH specimen data).

Group: Sample size	<i>iliaca</i> <i>n</i> = 11	<i>unalaschensis</i> <i>n</i> = 52	<i>schistacea</i> <i>n</i> = 20	<i>megarhyncha</i> <i>n</i> = 90
Wing-chord	88.5 (86.0–90.0)	81.2 (74.5–86.0)	80.6 (77.0–86.0)	82.5 (77.0–88.0)
Tail	71.7 (69.2–73.8)	73.7 (67.0–80.5)	79.0 (76.0–88.0)	84.8 (78.0–91.0)
Exposed culmen	11.6 (11.0–11.8)	12.0 (10.8–13.0)	11.0 (10.0–11.8)	13.3 (11.0–16.0)
Bill depth ¹	9.4 (9.4–10.0)	9.8 (8.5–11.0)	9.5 (8.8–10.2)	12.9 (10.5–15.5)
Bill width ²	8.2 (8.0–8.5)	8.2 (7.2–9.0)	8.0 (7.5–8.5)	11.0 (9.0–13.0)
Tarsus	24.2 (23.2–25.0)	25.0 (23.5–27.0)	23.2 (22.0–24.2)	24.0 (22.0–26.0)
Mass	36.1 (28.5–43, 46)	36.1 (31–44, 34)	30.4 (26–35, 28)	32.5 (29–38, 11)

¹Base of culmen to lower edge of mandible.

²At base of lower mandible.

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